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FACTORS INVOLVED IN THE APPLICATION OF FORM-CLASS VOLUME TABLES [1]

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INTRODUCTION

A method of constructing generalized taper charts and volume tables, based upon a formula for the stem curve and developed in its general principles from the form-class system used in Sweden, has been outlined in a previous paper by the writer (*2*).[2] In applying these generalized taper charts and volume tables to the measurement of stands of timber of any given species, the necessary steps are: (1) To study the variability of the form quotients of the trees in a stand in order to ascertain whether a single average form quotient may be used for the entire stand; (2) to work out a method of determining the average form quotient of the stands to be estimated in the field so that the proper form-class table may be selected for each set of conditions; and (3) to study the relation between normal diameter inside bark at breast height (4.5 feet above the ground) and the actual breast-height diameter for the species in question.

Some suggestions in regard to each of these three processes as well as references to the earlier literature were included in the previous paper. Since the problems referred to are inherent in the timber itself and are not peculiar to the form-class system alone, they enter into the application of volume tables of any sort and so merit intensive analysis. In this paper are presented the results of detailed statistical studies of these questions for red spruce (*Picea rubra* Link), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.) in the Northeast. Wright (*9*) studied these questions for the coniferous species of eastern Canada, but his results are not directly comparable to those given in this paper, primarily because he did not eliminate the effect of butt swell on diameter at breast height before determining form quotient. Furthermore, his data for spruce and fir were obtained from not more than eight stands for any one species, so that his method of approach was necessarily quite different. Gevorkiantz and Hosley (*4*), in their study of the form and development of white pine stands in Massachusetts, evolved a crown index, or measure of diameter of crown in relation to breast-high diameter of the tree, which when used in conjunction with the relative length of the crown provided a satisfactory basis for estimating form quotient.

Perhaps the most thorough investigations of variations in bark thickness in relation to form-quotient and volume estimation were those made by Heijbel (*6*) for Scotch pine in Sweden. He found

[1] Received for publication June 12, 1935; issued December 1935.
[2] Reference is made by number (italic) to Literature Cited, p. 713.

that the relative thickness of bark at breast height varied with the diameter of the tree, while bark thickness measured at one-tenth of total height was constant in all except the smallest size classes. He also found that for a given diameter class the shorter trees had relatively thicker bark. Scotch pines of low form class also appeared to have relatively thicker bark than those of higher form class. Heijbel proposes that bark thickness and volume determination be based on measurements at one-tenth the total height of the tree instead of at the fixed breast-height point.

In the study of the application of form-class methods to oak in Sweden, Hedeby (*5*) observed that form quotient of standing timber might be estimated from either the form point or relative length of crown, but that better estimates were obtained when diameter breast high was taken into consideration along with either of these factors.

In none of the studies reported has multiple-correlation technic been employed in attempting to evaluate the effect of various factors on form quotient, bark thickness, or butt swell.

BASIS AND METHODS OF STUDY

FIELD WORK

Distribution of Data

In order to study the effect of such stand factors as age, site index, density, and average height upon variations in average form quotient, or difference between normal diameter inside bark and actual diameters at breast height, it is necessary to obtain taper measurements on enough trees to give a satisfactory average in each of a number of stands representing the entire range of conditions to be considered. For this reason it was desirable to get samples from as many stands as possible, keeping the number of trees in each stand as low as was consistent with satisfactory accuracy of the averages. The desired degree of accuracy was set at a standard error of ± 1 unit in the average form quotient of the stand.

Data previously presented (*2*) and substantiated in this study indicate that the standard deviation of form quotients within a stand averages about 4.5 units. On this basis measurements of 20 trees are required to obtain an average with the desired accuracy of $\pm$ 1 unit. Increasing the number of trees to 30 reduces the standard error of the average from 1.0 to 0.82 units, and 40 trees only brings it down to 0.71 units, so that the gain in accuracy from the use of a larger number of trees must be balanced against the extra time required for their measurement.

Primary emphasis was placed on obtaining measurements in stands of even-aged second-growth timber, which lends itself much better than old growth to the evaluation of such factors as age, density, etc. Enough data were secured from old-growth stands, however, to afford a basis for studying the extent of variations of form within the principal types of the region and to indicate average form quotients that may prove generally applicable to these types, as well as to establish the relation between normal and actual diameters at breast height for timber of this character.

Measurements of 2,070 trees were taken in 74 stands scattered over northern New England and New York, covering a wide range of

mixture, age, site, and density. In stands in which any of the three species under study were present in mixture, samples were taken of each species. Except that obviously deformed or abnormal individuals were eliminated and an effort was made to cover the range of sizes present, trees were taken at random in each stand. In addition, data from 119 trees, measured by Meyer (*8*) as samples in connection with his study of yield of second-growth spruce and fir in the Northeast, were incorporated into this study. The distribution of these measurements of 2,189 trees among the various species and types of growth is shown in table 1.

TABLE 1.—*Basis for statistical analyses of trees*

Type of growth	Red spruce	White spruce	Balsam fir	All species
	Number	*Number*	*Number*	*Number*
Even aged	664	601	347	1,612
Old growth	345		232	577
Total	1,009	601	579	2,189

The ranges of age, site, and density covered by the samples for each species from the 74 different stands are shown in tables 2, 3, and 4.

TABLE 2.—*Distribution of sample stands by age classes*

Age (years)	Red spruce	White spruce	Balsam fir	Age (years)	Red spruce	White spruce	Balsam fir
	Number	*Number*	*Number*		*Number*	*Number*	*Number*
10–19	1	1		100–109	1		1
20–29	1	3	2	110–119			
30–39	1	9	4	120–129			
40–49	8	8	6	130–139	1		1
50–59	3	3	1				
60–69	6	3	1	Even-aged stands	31	28	17
70–79	5	1	1	Old-growth stands	17	0	11
80–89	2						
90–99	2			Total	48	28	28

TABLE 3.—*Distribution of sample stands by site classes*

Site index [1]	Even-aged			Old-growth	
	Red spruce	White spruce	Balsam fir	Red spruce	Balsam fir
	Number	*Number*	*Number*	*Number*	*Number*
30–34	1			1	
35–39	3		1	2	2
40–44	5	2	5	2	2
45–49	9	7	2	2	1
50–54	8	9	2	6	5
55–59	1	6	4	2	1
60–64	3	4	3	2	
65–69	1				
Total	31	28	17	17	11

[1] Based on average height of dominant trees and red spruce site-classification curves of Meyer (*8*). Site index of stands without red spruce expressed on basis of red spruce height growth by reducing white spruce heights 7 percent and balsam fir heights 9 percent.

TABLE 4.—*Distribution of sample stands by total number of trees per acre*

Trees per acre (number)	Even-aged			Old-growth	
	Red spruce	White spruce	Balsam fir	Red spruce	Balsam fir
	Number	*Number*	*Number*	*Number*	*Number*
100–199				1	
200–299		1		6	2
300–399	2	2	2	3	3
400–499	4	3	2		
500–599	3	2		1	1
600–699	4	4	2	2	2
700–799	5	1	1	1	1
800–899		2	1	1	1
900–999	2	4	2		
1,000–1,499	6	5	1	1	1
1,500–1,999	3	2	3	1	
2,000–2,499	2		1		
2,500–2,999		1	1		
3,000–3,999			1		
4,000–4,999		1			
Total	31	28	17	17	11

MEASUREMENTS TAKEN

In each stand in which measurements were taken a tally was obtained, either on a random strip survey or a rectangular sample plot, of the number of trees of each species by diameter classes. Descriptive notes covering history and general condition of the stand, underbrush, ground cover, soil, slope, injuries, site, etc., were also taken.

On each tree to be measured an estimate of form-point height as a percentage of total height was obtained with the aid of a hypsometer of the Christen type. Notes of crown class and shape of tip—flat, rounded, or pointed—were also made. In stands where the trees were being cut, total height and crown length were obtained with the tape as soon as the trees were felled; in stands where no cutting was being done, total height was measured with a Faustman hypsometer, and crown length as percentage of total height was measured with a Christen hypsometer. Heights were read to nearest foot. On each tree, age was obtained either from ring count on stump or from increment borings, usually taken 2.5 feet from the ground. Diameter measurements were obtained at stump (if cut), at 2.5 feet from ground, at breast height, and at one-twentieth, one-tenth, two-tenths, three-tenths, and each succeeding tenth of the stem between breast height and top as far as it was practicable to measure. On trees that were not cut, the taper measurements were not taken further than the seventh tenth above breast height. Measurements were taken with diameter tape to nearest tenth of an inch. At each point of diameter measurement thickness of bark was ascertained either with a hatchet and rule or by the use of a Swedish bark borer.

In a number of stands in which measurements were taken while pulpwood peeling operations were in progress diameter measurements inside bark were obtained directly from the peeled stems. In all such cases, breast-height diameter outside bark was taken and bark thickness was measured with the borer before peeling to provide a check on the accuracy of the bark borer.

Accuracy of Bark-Thickness Measurements

Analysis of 156 measurements taken on red spruce at time of peeling indicated that with the Swedish bark borer the thickness of bark of this species is underestimated, especially in old-growth timber. The standard error of the estimate of diameter inside bark from tape measurement outside bark reduced by use of the Swedish bark borer was ± 0.16 inch, and the average error was $+0.07$ inch. In 83 cases the errors in diameter were positive; in 25, negative; and in 48, no errors were indicated. The diameters included ranged from 6 to 23 inches.

From 33 balsam fir trees measured in this way no consistent bias was observed as a result of the use of the Swedish bark borer. The standard error of the inside bark diameter estimates was ± 0.08 inch.

Because a change from hatchet and rule to Swedish bark borer for determination of bark thickness was made after the first season's field work in this study, and because considerable differences appeared in the bark-thickness and butt-swell relations obtained from the data for the first 2 years, it seemed necessary to investigate the relative accuracy of the two methods of measuring bark thickness.

Measurements were obtained on 162 red spruce trees selected from a variety of stands in western Massachusetts, including both old growth and second growth. Diameters outside bark were taken with diameter tape. The bark of each tree was first measured with the Swedish bark borer at two points as nearly opposite as possible. The bark at points of measurement was then notched with a hatchet, and an average reading to nearest 0.05 inch was made with a steel rule.

The difference in double bark thickness was calculated for each point of measurement. These differences were grouped and averaged according to the diameters of the trees.

For the entire sample of 324 measurements the bark borer gave a double bark thickness averaging 0.077 inch greater than that given by the hatchet and rule. The difference tends to increase with the diameter of the trees, the coefficient of correlation being 0.456 ± 0.044. The average difference does not exceed 0.1 inch of double bark until trees are 13 inches d. b. h.,[3] and does not account for more than one-third of the spread noted in the bark-thickness and butt-swell relations of the data for the first 2 years of this study. On the whole, therefore, no importance need be attached to the difference between the two methods of measurement.

It seems quite certain, however, that the borer does give higher results than the hatchet and rule. Since it has been shown above that even the bark borer underestimates bark thickness in red spruce, it may be assumed that the bark borer gives the more accurate estimate of actual diameter inside bark. That the borer should be superior from this point of view is also evident from the fact that the bearing of the borer on the bark is directly comparable to the bearing of the caliper arm or tape, and the danger of flaking off is very slight. On the other hand, if the object is to get a true picture of actual thickness of bark, without respect to diameter measurements, the hatchet and rule, when carefully used, may be preferable. It is surprising how strongly the reading of the bark borer is affected by projections and irregularities of no real significance in judging actual

[3] Diameter breast high.

thickness of bark. Errors and abnormalities all tend to affect the reading in the same direction, so that there is no compensation whatever except the chance that the borer is not driven to the wood, and with careful manipulation there should be no danger of this. With the hatchet and rule, however, the bark is exposed in cross section for 2 or 3 inches and a reliable figure can be obtained if proper care is taken to avoid losing bark scales in chopping.

OFFICE WORK

Preliminary Calculations

A taper curve of diameter inside bark and height above ground was plotted for each tree. Wherever the reverse curve of the root swell extended above breast height the normal convex curve of the middle portion of the stem was continued downward to breast height, and from this was read the "normal" diameter of the tree. Whenever the measurement at half height was clearly erratic or out of line with those above and below, it was modified by reading a new value from the smooth curve drawn through the other points. From the figures thus obtained the amount of butt swell at breast height, the normal form quotient, and the percentile tapers of each tree were computed.

For each separate locality or stand the average age, form quotient, form-point height, and average height of dominant and codominant trees were computed from the trees measured in that stand. The standard deviation of the form quotients of the trees measured in each stand was also calculated. For each stand the total number of trees per acre, the number of trees more than 3 inches in diameter, and the percentage of each species were calculated from the strip survey or sample-plot tally sheets.

Check on Form Curve and Butt Swell Allowance by Localities

To aid in analyzing errors in volume tables, check the graphical elimination of butt swell and obtain further information upon the differences in average form curve in stands of different characters, a study was made of the fit of the material from each locality to the formula $y=\frac{x}{a+bx}$, in which y is the ratio of the diameter at distance x from the tip to the normal diameter at breast height, the distance x being expressed as percentage of total height above breast height. This formula when converted to the form $\frac{x}{y}=a+bx$, becomes the equation of a straight line.

For this purpose the percentile tapers of all the trees of each species in a locality were averaged and values of x/y were computed for the resulting average taper series. These values were then plotted x/y on x and conformity to a straight line noted.

The butt-swell eliminations were generally satisfactory, as shown by the breast-height point of the averages falling in line, and no good reason was found for modifying the graphs of the individual trees in the case of a few averages in which the results were not exact. There is, perhaps, a tendency to overestimate the butt swell in stands of very low form quotient.

The fit of the form curve in even-aged red spruce was good in general, but there was some tendency for the upper sections to fall below values given by the formula. The same applied to the old-growth red spruce, in which, however, the falling off in the tops was somewhat more common and more pronounced.

The even-aged balsam fir fitted very well in general, except in the swamp localities where the tops fell below the formula. In old-growth balsam fir the form curve varied systematically from the formula, the diameters being relatively larger below the mid-point and smaller above, resulting in a characteristic S curve for the plotting of x/y on x. Since the excess volume below the mid-point offsets the deficiency above, the effect on cubic volume is of no greater importance than in the cases of red spruce and even-aged balsam fir, which fitted better.

White spruce, on the whole, fits the formula better than either of the other two species. With this species the minor variations appear to be more or less definitely related to certain stand characters. Old-field stands fit very well when uniformly stocked. In extremely irregular stands the diameters in the tops do not hold up to the formula values, and in fully stocked natural second growth not of the old-field type the tops exceed the formula somewhat, except in the very young age classes.

The average taper series for each locality was then plotted x^2 on y and the corresponding absolute form factor obtained by planimetering the area under the curve. The differences between the actual absolute form factors thus obtained and the absolute form factors based on the formula corresponding to the average form quotients of the localities were then used to evaluate the effect of variation from the formula in terms of volume. Significance of errors was computed on the same basis as outlined in connection with table 6 of the writer's previous paper *(2, p. 716)*. Any error was considered significant which exceeded the probable error in volume resulting from normal variation of upper diameters within a form-class range of five units as calculated for the number of trees in the sample.

In general the fit was good and the significant volume errors ran above 2 percent in only a few cases. A summary of the results is given in table 5.

TABLE 5.—*Number of stand samples exhibiting significant volume errors of various magnitudes when measured by formula* $y=\frac{x}{a+bx}$

Significant volume errors (percent)[1]	Even-aged			Old-growth		All stands
	Red spruce	White spruce	Balsam fir	Red spruce	Balsam fir	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
0	16	12	7	3	3	41
0.1–1.0	4	13	8	5	7	37
1.1–2.0	10	2	1	7	1	21
2.1–3.0	0	0	1	2	0	3
3.1–4.0	1	1	0	0	0	2
Total	31	28	17	17	11	104

[1] Errors in excess of probable error resulting from normal variation of upper diameters within a form-class range of 5 units.

Coding and Machine Tabulation for Multiple-Correlation Studies

To facilitate sorting and tabulating by the use of punch cards and Hollerith automatic machines, all the data to be used in multiple correlation calculations were coded. Species, localities, types, and crown classes were given arbitrary numbers to permit sorting on these factors, and the values for all the other variables were grouped so that the entire range would be included in from 10 to 30 code numbers.

The average height of dominant and codominant trees of red spruce at 50 years of age according to Meyer (*8*) was used as the basis for site classification of the various stands. Stands in which no red spruce occurred were converted to the red spruce standard by reducing heights of white spruce 7 percent and of balsam fir 9 percent, these factors also having been determined by Meyer in connection with his study of the yield of these species. For coding, the site indices were grouped into classes of 2 feet each.

Average heights of dominants and codominants were grouped into classes of 3 feet each. Numbers of trees per acre were coded in hundreds, and average ages were coded in groups of 5 years each. The standard deviations of form quotients in each stand were grouped into classes of 0.2 units each.

The crown lengths of the individual trees expressed as percentages of total height were coded in 10-percent groups. Form quotients were thrown into groups of 3 units each, and form points, calculated down from tip in percentage of total height, were grouped by 5 units each. Total heights were coded in 5-foot groups, and breast-high diameters in even inch classes. Double bark thickness, butt swell, and the sum of these two factors were coded directly in tenths of inches.

The procedure outlined by Smith [4] for the solution of multiple correlation problems from punch-card tabulating-machine data was used throughout. In this work each species was kept separate, and old growth was kept separate from second growth. A list of all the data on all the cards was also run off on the machine to be used in checking errors in card punching, etc.

Smith's procedure for obtaining the coefficient for normal equations consists of the following steps:

1. Obtain mean of each variable from sum of all values and the number of observations.

2. Sort cards on first variable and tabulate the sums of all variables by this classification with count of numbers of observations in each class.

3. Multiply sum of each variable by class value of the sorted variable and add the products thus obtained. This gives the factors sum A^2, sum AB, sum AC, etc., from the arbitrary origin 0.0.

4. Sort cards on second variable, and in same manner as for first sorting obtain the factors, sum AB, sum B^2, sum BC, etc.

5. Repeat for all remaining variables.

[4] Smith, B. B. The use of punched card tabulating equipment in multiple correlation problems. U. S. Dept. Agr. 24 pp. 1923. [Mimeographed.]

6. For each of the above sortings, multiply sum of sorted variables by means of all others. This gives products of the form sum x. y_o which is equivalent to $N(x_o y_o)$ since $\frac{x_o = \text{sum } x}{N}$. In this notation the subscript "o" denotes the mean.

7. Subtract products obtained in 6 from corresponding product sums obtained in 3, 4, and 5. This gives the product sums about the means of the variables as origins, and these are the coefficients needed for the solution of multiple-regression equations.

The procedure as given by Smith assumes that for any observation of one variable there will be corresponding observations of all the other variables under consideration. In assembling the data for this study there were a number of instances where observations on certain of the variables were not available. For this reason it became necessary to modify the calculation of the coefficients for factors involving these variables.

Adjustment of Calculations for Variables with Incomplete Data

Using a general notation in which x= a variable for which a smaller number of observations, N^1, is available than in the case of y and other variables in the study, for which we have N observations, steps 3, 4, and 5 outlined above will give factors of the form sum xy composed of only N^1 products in all cases involving the short variable x.

For step 6 in the above outline with respect to variable x, determine first the true mean of this variable, which will be $\frac{\text{sum } x}{N^1}$. Then obtain from the machine tabulation in which the sorting was done according to x the sums of the other variables for observations actually paired with observations of x. Multiply these sums by the actual mean of the variable x, which will give factors of the form $N^1(x_o y_o)$. These are to be subtracted from the products sum xy obtained in steps 3, 4, and 5. In order to use the coefficiens thus obtained on the basis of N^1 observations in multiple correlation with other variables whose coefficients are based on N observations we must assume that the magnitude of the coefficients would be proportional to the number of observations. The coefficients for all factors involving the variable x must therefore be increased by the factor $\frac{N}{N^1}$. This assumption should not involve much danger so long as N^1 is not much smaller than N.

If more than one variable is incomplete, special care must be taken to use the proper figures in the calculation of the coefficient for the product of a pair of short variables. The correct number of cases in which the two short variables are actually paired must be ascertained, and this must be used to obtain, in conjunction with the sums of the variables in these cases, the true means of the variables, and also in making the final adjustment of the coefficient to place it on the basis of N observations.

In the present study this adjustment had to be made in the cases of crown length and form quotient based on the entire stem, but since the latter was not used in the final analyses, it affects only those relations in which crown length appears as a factor.

FACTORS OF AVERAGE FORM OF STANDING TIMBER

VARIABILITY OF FORM QUOTIENT

The present study substantiates the conclusions drawn in a previous paper (*2*) that a standard deviation of about ±4.5 units will apply quite generally as an average representation of the variability of form quotients within a stand. The range of variability found among the stands measured was quite high, as might be expected with figures for each stand based on only 20 trees (table 6).

TABLE 6.—*Variability of form quotients in stands*

Type and species	Stands	Average of standard deviation of form quotients in stands	Range of standard deviation of form quotients in stand	Standard deviation of form quotients of individual trees from all stands
Even-aged stands:	*Number*			
Red spruce	31	4.71	3.0–6.7	7.52
White spruce	28	4.24	2.8–6.6	7.57
Balsam fir	17	3.92	2.3–6.0	5.39
Old-growth stands:				
Red spruce	16	4.58	3.2–5.6	5.22
Balsam fir	11	4.80	3.2–6.4	5.63

The variability of form quotients in stands does not seem to be associated very closely with any factor which can be readily evaluated. The variability tends to decrease as the number of trees per acre increases and as age increases. Variability is usually less in stands of high average form quotient than in stands of lower average form quotient. In the case of even-aged red spruce and balsam fir the number of trees per acre has more influence on variability of form quotients than has age, site, or average height, but for white spruce age is the most important factor.

DETERMINATION OF AVERAGE FORM BY FORM-POINT METHOD

In the application of the form-class volume-table system in Sweden the form-point method has been used for estimating the average form quotient of the various stands. The form-point method has been described in detail by Jonson (*7*) and outlined by Wright (*9*) and Behre (*2*). In his previous paper (*2*) the writer worked out in detail the application of the form-point relation for western yellow pine, now known as ponderosa pine, and preliminary functions for red and white spruce and balsam fir were prepared for use by Meyer (*8*) in connection with his yield tables for these species. Wright (*9*) gives rectilinear form-point relations for white spruce, black spruce, and balsam fir, but since in each case these are based on the data from only one locality, and since they take no account of curvature, they cannot have any general significance. It has been found that species differ in their relations between form point and form quotient, so that in this study separate relations were worked out for each of the five sets of data.

In previous work rectilinear relations have been used even though some curvature was indicated, but it now appears that the curvature is not only consistent in all species and usually of sufficient amount to affect materially the accuracy of estimate, but that it is associated with

definite growth conditions and, therefore, should be taken into account. The relation between form point and form quotient in general is such that the closer the form point lies to the tip of the tree, the higher the form quotient. When averages of a large number of trees are plotted, however, it will be found that very little if any increase in form quotient will accompany a movement of the form point closer to the tip than 25 percent of the total height. In fact, especially with white spruce, it will be found that form points extremely close to the tip are often associated with relatively low form quotients. In the field it will be observed that trees on which the form point as usually defined falls within 15 percent of the tip are commonly tall, slim, intermediate trees with thin-foliaged crowns of very limited development. These trees are generally closely sheltered by adjacent crowns, and the crown surface presented to the wind is so small in comparison with crowns of more normally developed trees and in proportion to their total area including bole that it ceases to be the dominant element in determining form quotient. That relatively low form quotients should be associated with the narrow crowns of these trees in spite of extremely high form points is in accord with the findings of Gevorkiantz and Hosley (*4*), which indicate that form quotient may be estimated accurately from crown length and width.

The form-point relations are presented in figures 1 and 2, and the accuracy of estimates of form quotients from these curves is shown in table 7.

TABLE 7.—*Accuracy of estimates of form quotients from form point*

Type and species	Standard deviation of form quotients	Accuracy of estimates of form quotient of single trees from form-point curves			Standard error of estimating average form quotient of stand from measurement of form point on 20 trees [1]	Number of trees required to attain standard error of average form quotient not over ±1 unit [1]
		Standard error	Alienation index	Index of determination		
Even-aged stands:						
Red spruce	7.52	5.00	0.66	0.56	1.54	48
White spruce	7.57	5.04	.67	.55	1.47	44
Balsam fir	5.39	4.28	.79	.38	1.30	34
Old-growth stands:						
Red spruce	5.22	4.72	.90	.19	1.47	44
Balsam fir	5.63	4.52	.80	.36	1.47	44

[1] Based on formula $_{SD}\sigma_{\bar{x}_1}=\sqrt{\frac{_{SD}x^2+_{SD}d^2}{N}}$

in which—
$\sigma_{\bar{x}_1}$=average of observed deviations.
x=true deviation ($_{SD}x$ from table 6, column 3).
d=error of observation ($_{SD}d$ from column 3, above).
N=number of observations.

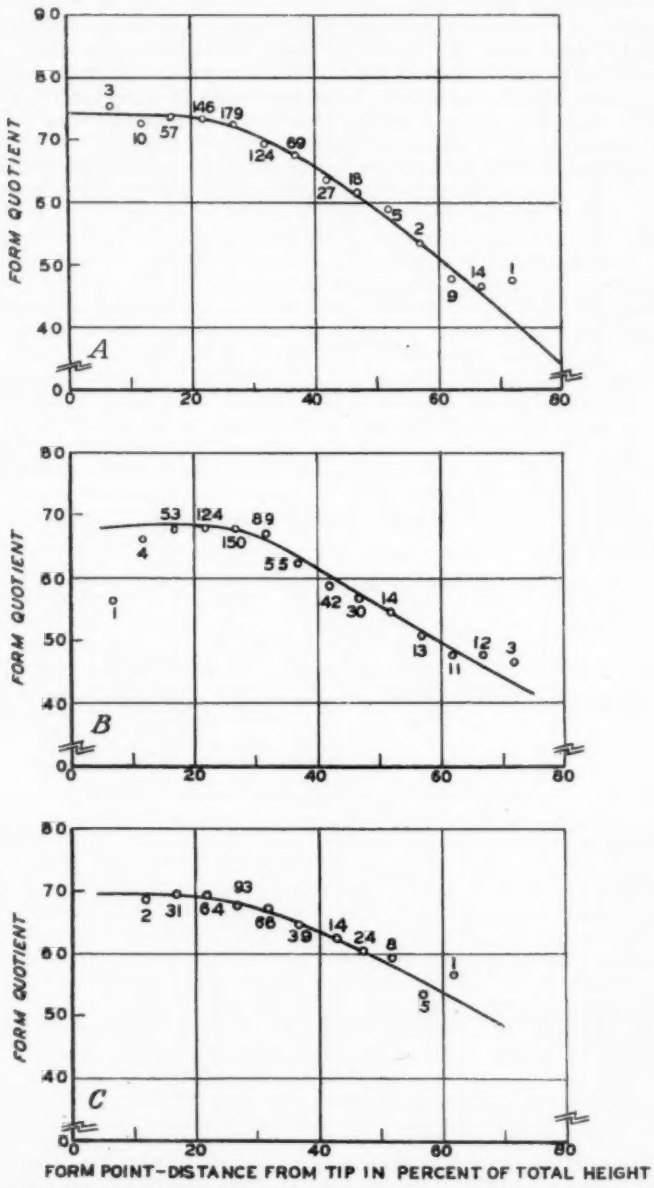

FIGURE 1.—Relation of form quotient to form point in even-aged stands: *A*, Red spruce; *B*, white spruce; *C*, balsam fir.

It will be seen from table 7 that although the standard errors [5] of estimating the form quotients of individual trees from the form-point relations vary less than one unit between the five sets of data, yet there is a big difference in the alienation indices [6] because of con-

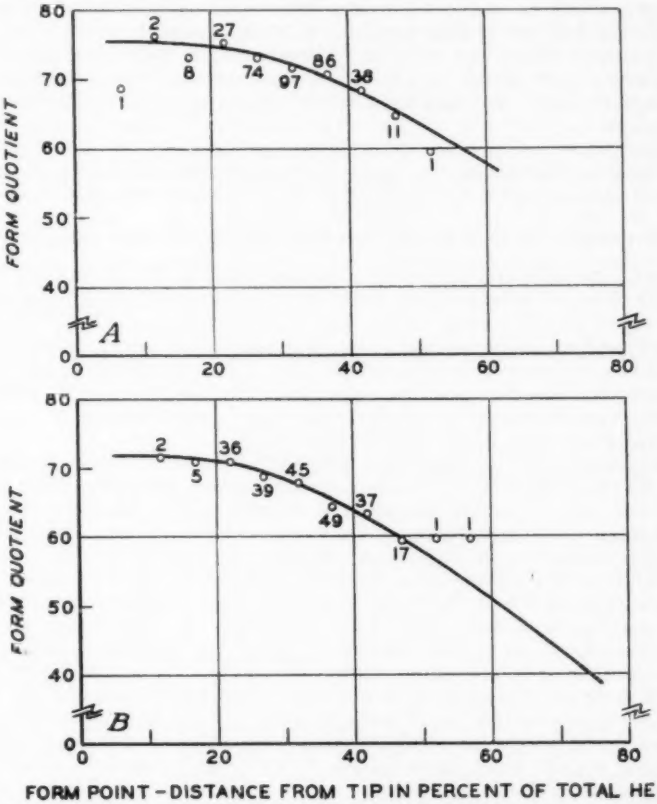

FIGURE 2.—Relation of form quotient to form point in old-growth stands: *A*, Red spruce; *B*, balsam fir.

siderable difference in the initial variability of the form quotients. Thus, although the use of form point reduced the variability of

[5] The standard error of estimate is the standard deviation of the differences between the actual values of the dependent variable and the corresponding values as estimated from a curve, a regression equation, or an alinement chart. It measures the variation about the average relationship in absolute terms.

[6] Alienation indices are used in this study as the primary measure of correlation. The alienation index is the ratio between the standard error of estimate of a dependent variable from any set of independent variables and the original variation of the dependent variable; thus $AI=\frac{SE_{y.abc...}}{SD_y}$ When the relationships are rectilinear the term "alienation coefficient" is used instead of alienation index. The alienation index is an abstract measure of the degree of relationship. Its chief merit is the fact that it gives a direct percentage measure of the improvement in estimating one factor from any functional relationship in which it may be involved. The index of determination is perhaps a better measure of the proportion of variation of the dependent variable which is associated with the independent factors which have been included in any problem. The index of determination is the square of the index of correlation and its relation to the alienation index is such that $CI^2+AI^2=1$. In this paper indices of determination are given in each table along with alienation indices, in order to facilitate interpretation, no matter which measure the reader is accustomed to use.

estimate of individual form quotients about one-third in the case of even-aged red spruce and white spruce it fails to account for more than one-tenth of the error of estimate of form quotients in old-growth red spruce. On the other hand, it has been found (table 6) that the variability of form quotients in any single stand of old-growth red spruce will be about 4.6 units. The total variability of all the old-growth red spruce data was only 5.22 units, which, being so near 4.6, indicates that there could not have been any great difference in the average form of the various stands measured as compared to the even-aged stands, the data from which showed a total variability of 7.52 units.

With these species, just as with ponderosa pine (*2*), form point must be measured on approximately 45 trees in order that the standard error of the average form quotient be kept down to ± 1 unit.

DETERMINATION OF AVERAGE FORM FROM STAND AND TREE FACTORS

One of the principal objects of this investigation was to find out by statistical means whether form quotient was associated closely enough with any of the characters of the stand or of the trees so that it could be derived from measurements that are usually obtained during the course of a cruise or tally of a sample plot. This would eliminate the necessity for introducing a new conception like the form point, which requires special attention in the field and is not subject to exact determination even when well understood.

The characters of the stand that lend themselves to numerical evaluation for this purpose are site index, average height, number of trees per acre, and age. Average height of dominant and codominant trees and number of trees 3 inches and more in diameter were selected as the best measures for expressing height and density respectively. For purposes of studying form, basal area per acre is of little value as an indication of density because, at a given age, density and average form may vary widely without much change in total basal area. Basal area tends to remain constant because an increase in average size accompanies reduction in number of trees per acre. Number of trees 3 inches and more in diameter was found by statistical tests to be superior to total number of trees per acre for form studies, probably because it eliminates the comparatively large number of smaller trees in young stands that have ceased to exert any real influence on development of the future stand.

The measurable tree characters that may affect form quotient are diameter, height, length of crown, width of crown, and crown class. In planning this study it was thought that width of crown would be impractical to measure in the field, because of irregularity of crown outline, interlacing of adjacent crowns, and inaccessibility or invisibility of points of measurement, so no data were obtained on this factor. In the light of subsequent work in northern white pine by Gevorkiantz and Hosley (*4*) indicating the usefulness of crown width measurements in conjunction with crown or dead length, it is to be regretted that these measurements were omitted.

Analysis of Tree Factors

Correlation calculations involving various combinations of both stand and tree characters were used as a means of determining how each numerically measured factor is related to form quotient and

which of these factors have significant influence on the variation of form quotients among the individual trees. From multiple regression equations [7] involving all the variables and affording some preliminary idea of the relative weight of each factor, it appears that diameter breast high, height, crown length, and site are the most important factors.

Multiple correlations involving form quotient and the four factors mentioned above were computed for the even-aged material and corrected for curvature by the method of Bruce and Reineke (*3*). The alienation indices and indices of determination are given in table 8. They represent the highest practical degree of accuracy that may be attained in the estimation of form quotient of individual trees. They mean that diameter breast high, height, crown length, and site together may account for 64 percent of the variability of individual form quotients in even-aged red spruce, for 66 percent in white spruce, and for 42 percent in even-aged balsam fir. More than a third of the total variability of form quotient is apparently associated with other factors and probably is not readily susceptible to numerical evaluation.

TABLE 8.—*Accuracy of estimates of form quotients from individual tree factors*

Type and species	Factors with which form quotient is correlated							
	Diameter breast high, height, crown percent, and site index		Crown percent		Diameter and height		Diameter, height, and crown percent	
	Alienation index [1]	Index of determination [2]	Alienation index	Index of determination	Alienation index	Index of determination	Alienation index	Index of determination
Even-aged stands:								
Red spruce	0.60	0.64	0.69	0.53	0.73	0.46	0.64	0.59
White spruce	.58	.66	.62	.61	.64	.59	.58	.66
Balsam fir	.76	.42	.81	.35	.81	.34	.76	.42
Old-growth stands:								
Red spruce			.88	.23	.90	.20	.80	.36
Balsam fir			.75	.44	.88	.23	.75	.44

[1] $\sqrt{1-CI^2}$.
[2] CI^2.

Study of the regression coefficients [8] and curves of net regression [9] in the several multiple correlations worked out show that diameter

[7] Rectilinear functions fitted to the data by the method of least squares. Multiple regression equations express the function of a dependent variable in terms of any number of independent variables, without allowing for curvature in any of the individual relationships. They take the general form $y=ax_1+bx_2+cx_3+ \ldots +N$.

[8] In a regression equation of the form $y=ax_1+bx_2+cx_3+ \ldots +N$, the constants a, b, c, etc., are the regression coefficients of the several variables. The relative weight of each variable is indicated in a rough way by the size of these coefficients in relation to the absolute values of the different variables. Obviously the value of y in the regression equation will be more strongly influenced by a variable with a large regression coefficient than by one of about the same absolute value with a low regression coefficient. On the other hand, a low regression coefficient for a variable of large absolute values may have more weight than a large regression coefficient for a variable which never attains a high absolute value. But only a crude idea of relative weight may be obtained from the regression coefficients and absolute values because the rectilinear equation may distort badly the actual influence of any factor in respect to which the relationship is curved.

[9] Net regression of any independent variable in multiple correlation is the relation between that variable and the dependent variable when the other independent variables are held constant at their means. Net regression curves are obtained by plotting the residuals of estimates of the dependent variables from the multiple regression equation around the original net regression line for each variable. The slope, degree of curvature, and closeness of fit of the net regression curves afford some indication of relative weight of the variables and may be used to supplement a study of the regression coefficients.

and height have substantially greater weight than the other factors but, having opposite signs, tend to compensate. This compensation is especially significant because there is a close association between diameter and height.

Examination of the deviations from the net regressions of form quotient on height indicate that form quotient increases rather rapidly with height until trees are about 40 feet tall, after which there is little further increase except in the case of white spruce, where it continues at a lower rate.

Data sorted by diameter classes show form quotients to be at a maximum at about 7 inches diameter in even-aged stands and at 8 or 9 inches in old growth. In the even-aged data the slope away from the maximum in either direction is relatively steep, each inch of diameter indicating a decrease of from 1 to 2.2 units of form quotient. In the old-growth data this decrease is much more gradual. The same tendencies appear in the plotting of deviation from the net regression of form quotient on diameter in multiple correlation with other variables.

This indication of a definite correlation between form quotient and diameter deserves further consideration, because previous work (*2*) had indicated that within stands the correlation between diameter and form quotient was so slight that an average form quotient could be safely used for the entire stand.

In order to study this point further, it was necessary to correlate deviations from mean form quotient with deviations from mean diameters within stands rather than to consider the association of form quotient with diameter breast high for the entire mass of material. Since the trees measured in each stand were arbitrarily selected to cover the range of sizes and crown classes exhibited rather than to give a weighted average for the stand, it was deemed advisable to use approximate median values as the basis for this calculation rather than the average of the trees that happened to be included in each stand sample. A composite sample of 5 to 10 stands taken at random from the available data was used for each species. In each case a significant but small negative correlation was obtained. The results are summarized in table 9. Although only 4 to 19 percent of the variation of the individual form quotients, as judged by the coefficients of determination, is associated with the size of the trees with reference to the medians for each stand, yet there will generally be a range of 6 to 15 units between the average form quotient of the smallest trees in a stand and the average of the largest. This is consistent with Wright's findings (*9*), although the differences he observes are exaggerated by the fact that root swell at breast height lowers the form quotients of the larger size classes abnormally in his calculations.

Similarly, if deviations from mean form quotient in each stand are averaged by crown classes there appears a definite tendency for the dominant trees to be lower in form quotient than either codominant or intermediate trees. Suppressed trees also average lower than intermediates, but not generally as low as the dominants. This tendency is most pronounced in red spruce where there is a range of between 2 and 3 units of form quotient between the dominant and codominant or intermediate trees in both old growth and second growth. It is of no significance in white spruce, where the range is only about 1 unit of form quotient.

TABLE 9.—*Correlation of form quotient with diameter within stands*

Type and species	Coefficient of correlation	Standard error of coefficient of correlation	Coefficient of determination	Alienation coefficient	Regression coefficient	Approximate range of average form quotient by diameter classes	Basis	
							Stands	Trees
Even-aged stands:							*Number*	*Number*
Red spruce	−0.439	±0.057	0.193	0.898	−1.131	15	10	200
White spruce	−.377	±.061	.142	.926	−.825	9	10	201
Balsam fir	−.415	±.083	.172	.910	−1.124	6	5	100
Old-growth stands:								
Red spruce	−.420	±.082	.176	.908	−.668	12	5	100
Balsam fir	−.205	±.081	.042	.979	−.668	6	6	139

If the data are sorted by crown classes without respect to the individual stands, this tendency appears to be more pronounced, dominant trees averaging from 3 to 5 units lower in form quotient than intermediate trees, with the codominant class generally between these extremes. In no case, however, does consideration of crown class reduce the variation of form quotients more than 5 percent.

The variation of form quotients within stands is also associated with differences in the crown lengths of the individual trees. When deviations from median form quotients within stands are correlated with deviation from median crown percentages, it is found that the longer the relative length of crown the lower the form quotients (table 10). For red spruce and white spruce the trees with shortest crowns will average 7 to 8 units higher in form quotients than those with the longest crowns in the same stand. With even-aged balsam fir this relation has no significance, while in old-growth balsam fir it is much more definite than on either of the other species. This is interesting when considered in relation to table 9, in which old-growth balsam fir shows the least significant relation with diameter.

TABLE 10.—*Correlation of form quotient and crown percent within stands*

Types and species	Coefficient of correlation	Standard error of coefficient of correlation	Coefficient of determination	Alienation coefficient	Regression coefficient	Approximate range of average form quotient by crown-percent classes	Basis	
							Stands	Trees
Even-aged stands:						*Form quotient units*	*Number*	*Number*
Red spruce	−0.367	±0.061	0.135	0.930	−0.161	7.5	10	200
White spruce	−.375	±.061	.141	.927	−.166	8.0	10	201
Balsam fir	−.110	±.099	.012	.994	−.045	1.5	5	100
Old-growth stands:								
Red spruce	−.302	±.090	.091	.953	−.134	7	5	102
Balsam fir	−.450	±.068	.203	.893	−.147	6	6	139

Crown percent is the only factor showing any appreciably crude correlation with form quotient when all the data for each species are thrown together; and indeed when the function is curved (figs. 3 and 4) the result is slightly better than when estimates of form quotient are based on diameter and height together (table 8), and about the same as that obtained by the use of form point (table 7). Wright (*9*)

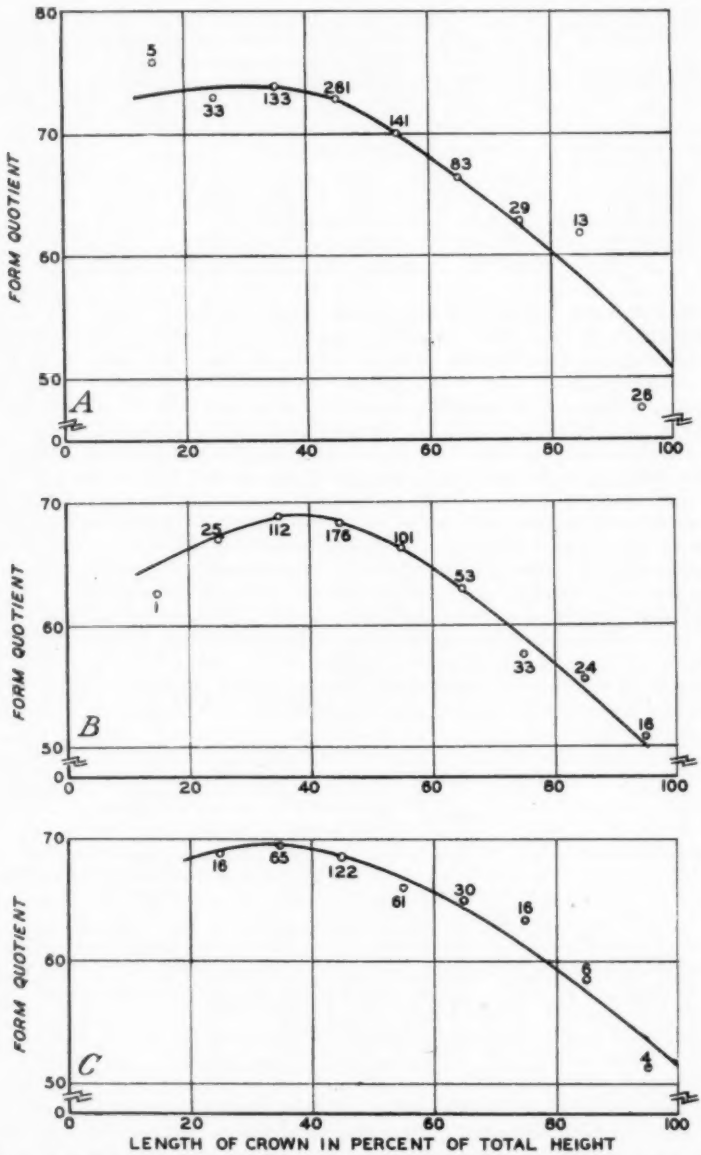

FIGURE 3.—Relation of form quotient of individual trees to crown length in even-aged stands: *A*, Red spruce; *B*, white spruce; *C*, balsam fir.

and Hedeby (*5*) also concluded that relative length of crown afforded as satisfactory a basis for estimating form quotient as the form point. Form quotients generally reach a maximum in trees with crown lengths about 40 percent of total height. With crowns longer than

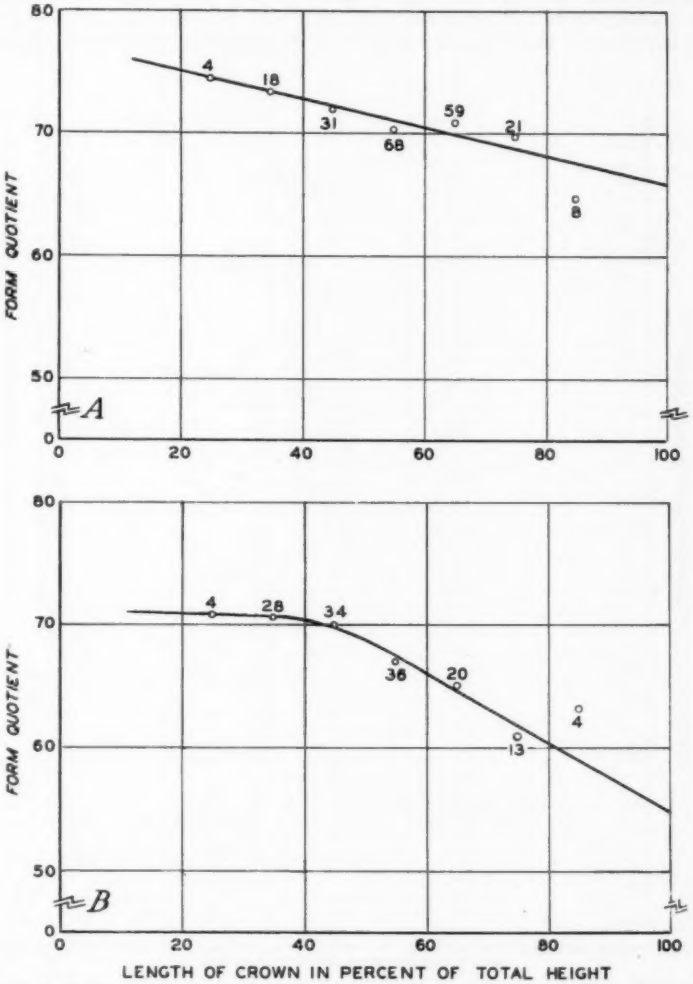

FIGURE 4.—Relation of form quotient of individual trees to crown length in old-growth stands: *A*, Red spruce; *B*, balsam fir

this there is a definite and steady decrease of form quotient and, just as was the case for trees with extremely high form points, form quotients average less than the maximum when crown length is less than 30 to 40 percent of total height.

From estimates on the basis of diameter, height, and crown percent, it will be seen (table 8) that, for white spruce and balsam fir, the results are just as good as when four factors were used, and that for red spruce they are within 4 percent of that accuracy. It would seem, therefore, that the fourth factor, site index, might be dropped as having little influence on form quotient beyond that which may be involved in the diameter-height-crown length relationship. What-

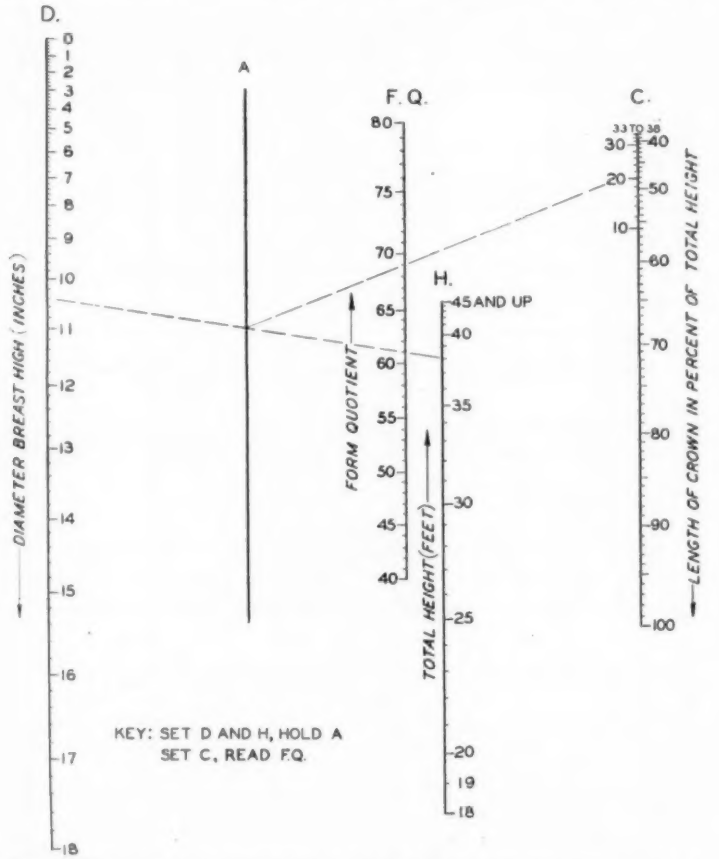

FIGURE 5.—Alinement chart for estimating form quotient of red spruce in even-aged stands from diameter, height, and crown length of individual trees.

ever influence site index may have appears to cause trees on poorer sites to average higher in form quotient than do those on the better sites. That there is such a relationship is evidenced by the fact that estimates of form quotient based on diameter, height, and site index are almost as satisfactory as those based on diameter, height, and crown percent, especially in the case of even-aged red spruce, but it has not seemed possible to break down the interrelations between the

various factors to show definitely which elements may be the more fundamental.

Alinement charts for estimating form quotient from diameter, height, and crown percent are given in figures 5–9, and data indicating

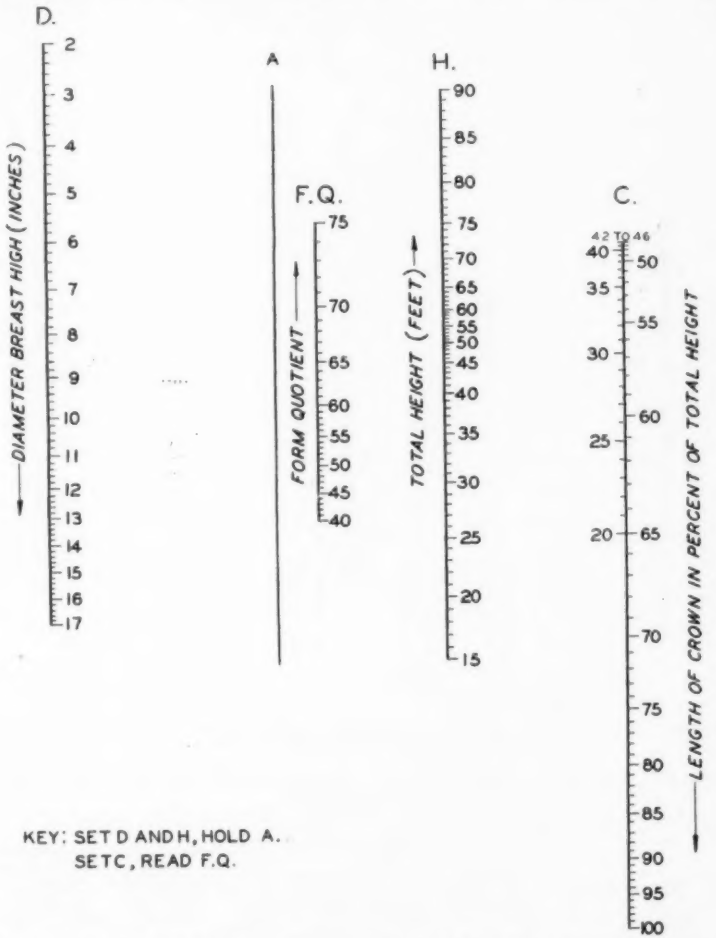

FIGURE 6.—Alinement chart for estimating form quotient of white spruce in even-aged stands from diameter height, and crown length of individual trees.

the accuracy of estimates from these charts are given in table 11. The results are somewhat better than those obtained by the form-point method (table 7) or from crown percent alone (table 8), but to obtain an average stand form quotient with standard error not over ± 1 unit still requires the measurement of about 40 trees.

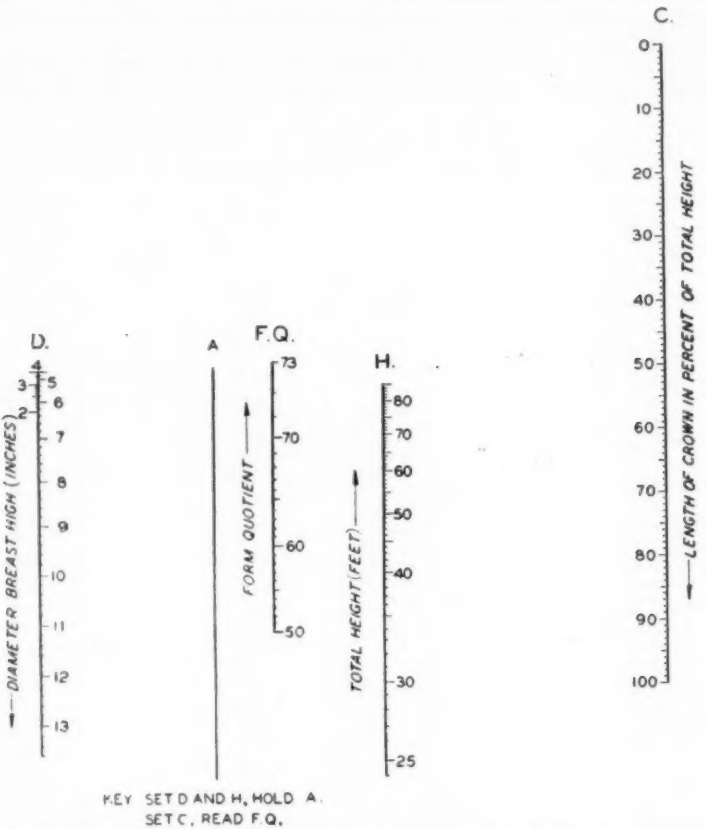

FIGURE 7.—Alinement chart for estimating form quotient of balsam fir in even-aged stands from diameter, height, and crown length of individual trees.

TABLE 11.—*Accuracy of estimates of form quotient from diameter breast high, height, and crown percent*

Type and species	Standard deviation of all form quotients	Accuracy of form quotient estimates of individual trees			Standard error of average form quotient of stand based on estimate of 20 trees [1]	Trees required to attain standard error of average form quotient not over ±1 unit [1]
		Standard error	Alienation index	Index of determination		
Even-aged stands:						*Number*
Red spruce	7.52	4.81	0.64	0.59	1.51	46
White spruce	7.57	4.39	.58	.66	1.36	38
Balsam fir	5.39	4.10	.76	.42	1.27	33
Old-growth stands:						
Red spruce	5.22	4.19	.80	.36	1.39	39
Balsam fir	5.63	4.24	.75	.44	1.43	42

[1] Based on formula $\sigma x_1 = \sqrt{\frac{SD_x^2 + SD_d^2}{N-3}}$ in which—

σx_1 = average of observed deviations.
x = true deviation (SD_x from table 6, column 3).
d = error of observation (SD_d from column 3 above).
N = number of observations.

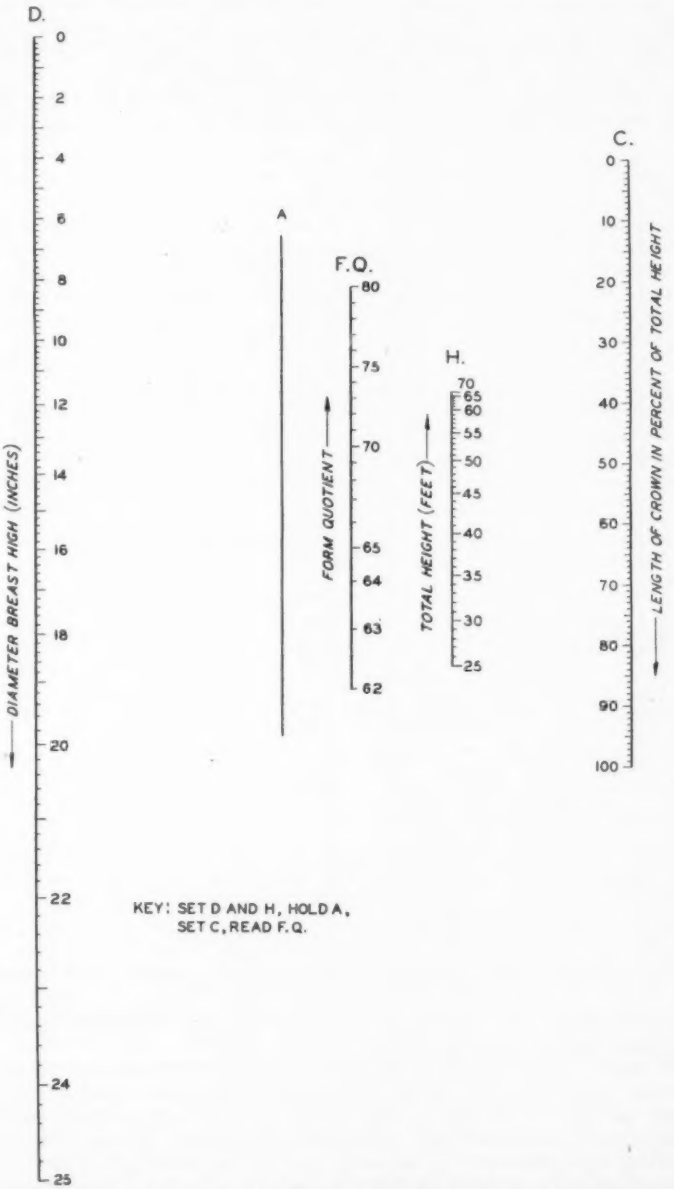

FIGURE 8.—Alinement chart for estimating form quotient of red spruce in old-growth stands from diameter, height, and crown length of individual trees.

To summarize these observations: It appears that variations in form quotient of individual trees are more closely dependent upon crown length than upon any other single factor and may be estimated on this basis just as well as by the form-point method. A more accurate estimate of form quotient may be obtained by considering diameter and height in conjunction with crown percent, and results

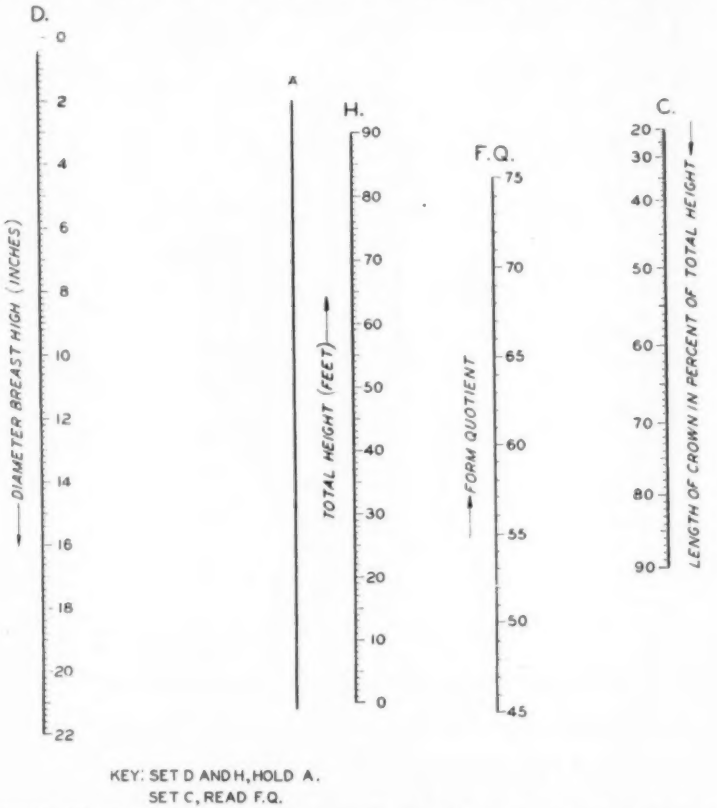

FIGURE 9.—Alinement chart for estimating form quotient of balsam fir in old-growth stands from diameter, height, and crown length of individual trees.

of about the same degree of accuracy may be obtained by using diameter, height, and site index.

Within the individual stands there is a slight but definite tendency for the larger trees or those with larger crowns to average lower in form quotient than the smaller ones or those with short crowns. Accuracy of estimates may, therefore, be slightly increased by subdividing the stand on the basis of size or crown length. But since this relationship is not very definite and since there is a compensation in that absolute form factors are not exactly proportional to form quotients (*2, p. 731*), it will seldom be necessary to apply this refinement in practice.

ANALYSIS OF STAND FACTORS

Since an average form quotient will generally be used for all the trees in each stand, it is desirable to investigate what association may exist between the characteristics of a stand and its average form quotient. Such a relationship may be more convenient to use than to estimate form quotient from a number of individual trees.

Because of the strong relationship already shown between crown percentage and form quotient, it is natural to suppose that the average form quotient of the stand would be closely associated with its relative crown length, which might well be measured as the average crown percent of the dominant and codominant trees. From table 12 it will be seen that 56 to 60 percent of the standard deviation and 81 to 84 percent of the variance of average form quotients of even-aged stands is associated with average crown percentages. The residual variation does not seem to be associated with either age, number of trees per acre, site index, height, or average diameter. The number of old-growth stands for which data are available is too small to yield any statistical expression of results, but for old-growth balsam fir only 1 of the 6 available stands varies more than 2 units of form quotient from a straight line fitted to the data. For old-growth red spruce, however, the points are more scattered although a similar trend is indicated.

TABLE 12.—*Accuracy of estimate of average form quotient of even-aged stands from average crown percent and from age and number of trees per acre more than 3 inches in diameter*

Species and number of stands	Standard deviation of average form quotients	Accuracy of estimates of average form quotient from average crown percent			Accuracy of estimates of average form quotient from age and number of trees per acre		
		Standard error	Alienation index	Index of determination	Standard error	Alienation index	Index of determination
Red spruce, 31	6.32	2.51	0.40	0.84	2.85	0.45	0.80
White spruce, 27	6.60	2.75	.42	.82	3.53	.53	.72
Balsam fir, 15	3.92	1.71	.44	.81	1.62	.41	.83

Further analysis of the even-aged material by Bean's method of graphical multiple correlation (*1*) shows that the average form quotient is also definitely correlated with age and number of trees per acre. Age is the more important factor, especially in earlier years of life. Up to about 70 years of age the average form quotient in even-aged stands of spruce and fir is increasing rapidly. After that time red spruce and balsam fir show little, if any, change in form, whereas in white spruce form quotient continues to rise but at a slower rate. Wright (*9*) states that form quotient increases with age up to about 50 years. The average form quotient also increases as the number of trees per acre of more than 3 inches in diameter increases, up to about 1,200. Beyond this density no increase is noted; in fact, in the case of balsam fir there is a slight tendency for stands with more than 1,200 trees per acre to have somewhat lower form quotients. Wright (*9*) also observed an increase of form quotient with density (basal area) within certain limits. Little improvement in accuracy is attained when average height or site index are taken into consideration.

Alinement charts for estimating average form quotient from age and number of trees per acre of more than 3 inches in diameter are given in figures 10, 11, and 12.

That variations in age and number of trees per acre reflect approximately the same condition as variations in average crown percent is evidenced by the fact that residuals from form quotients estimated from crown percent do not appear to be correlated at all with either age or number of trees per acre, and that estimates of form quotient from age and number of trees per acre can be only slightly improved by consideration of average crown percent.

Although these measures appear less accurate (table 12) than those based on characteristics of individual trees (compare standard errors of estimate with those in table 7 and table 11), the indices of determination are fairly high and it is probable that they will be just as satisfactory in practice.

For the many-aged and mixed stands of old growth characteristic of the spruce-fir forests, average crown percent is the only one of these factors having any significance, and, as already mentioned, the relation between form quotient and crown percent is not clear-cut in old-growth red spruce. However, the old-growth stands included in this study, as already pointed out (p. 682), show a relatively restricted range of variation in average form, and study of the characteristics of the individual stands reveals a fairly distinct grouping which should make it possible to assign each stand encountered in the field to its proper form class by inspection and without any measurements. Thus, old-growth red spruce falls into two groups as follows:

F. Q. 73 applies to old-growth red spruce in closed stands quite generally, whether pure or in varying mixtures with hardwoods. Swamp types with long narrow crowns and drooping branch habit (black spruce) also fall into this group.

F. Q. 70 applies to heavily culled or broken stands of spruce and hardwoods covering a wide range of sites and mixtures.

With old-growth balsam fir the distinction indicated for red spruce does not seem to hold, but all the stands group themselves around F. Q. 67, which may be taken as a general average, or average crown percent may be used to get a closer estimate.

This association of fairly constant average form quotient with easily recognized stand characteristics applicable over wide areas, is in accordance with previous observations of the writer (*2*) for ponderosa pine and of Wright (*9*) for northern white pine and black spruce. It should be noted that since Wright made no allowance for butt swell in the calculation of individual form quotients, it is not inconsistent that he should assign slow-growing black spruce to F. Q. 68, whereas the writer, having corrected for butt swell, places these stands in the F. Q. 73 group.

COMPARATIVE FORM OF SPECIES

In studying the conditions in the wide variety of stands included in this investigation, it soon became apparent that there were certain significant differences in form between the three species studied under identical stand conditions. The differences in question are not those arising from slight variations in type of stem form referred to under Check on Form Curve and Butt Swell Allowance by Localities (p. 675), but rather represent differences in form quotient or relative

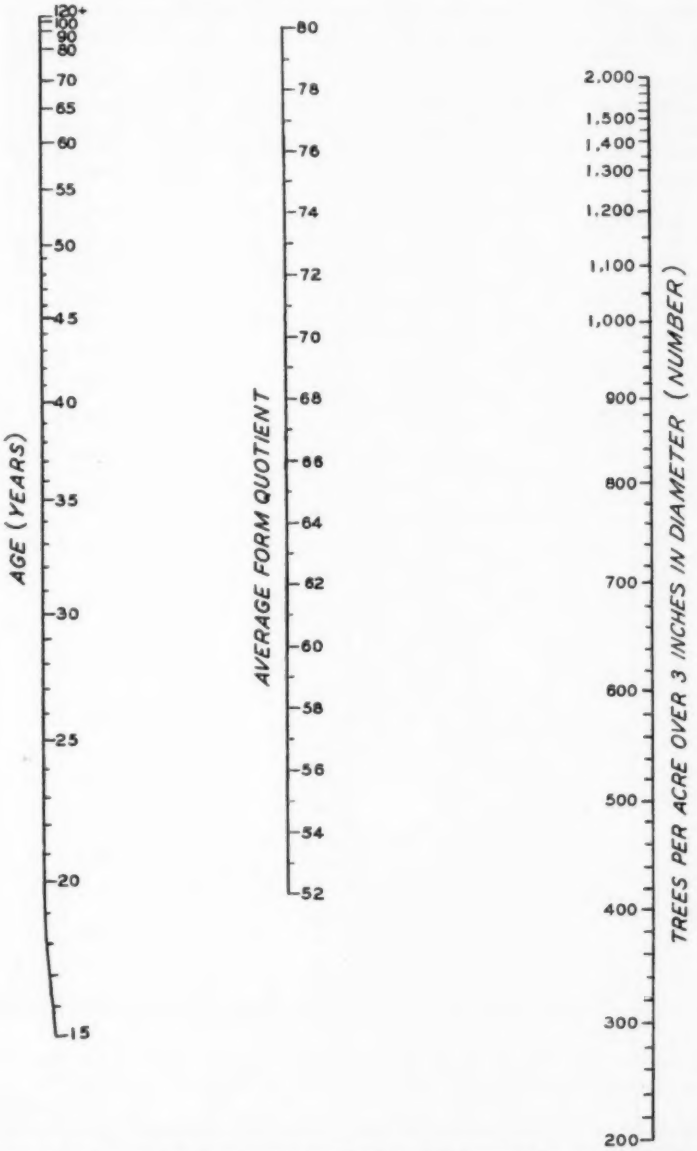

FIGURE 10.—Alinement chart for estimating average form quotient of even-aged stands of red spruce from age of stand and number of trees per acre over 3 inches d. b. h.

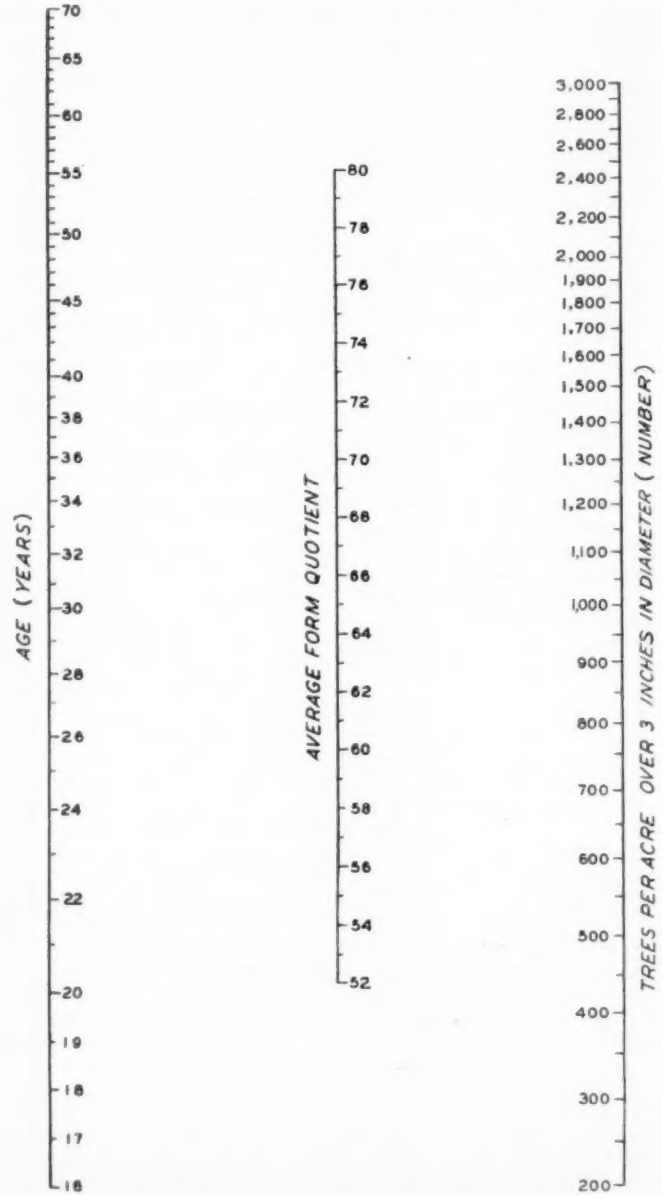

FIGURE 11.—Alinement chart for estimating average form quotient of even-aged stands of white spruce from age of stand and number of trees per acre over 3 inches d. b. h.

taper with the basic stem form essentially similar. Such differences are best illustrated by a comparison of the average form quotients in mixed stands.

Red spruce and balsam fir occur together quite generally in mixture with hardwoods in the old-growth stands of the region. Red spruce and balsam fir are also found quite frequently together in even-aged second growth. White spruce is absent from old-growth stands and occurs almost entirely in the even-aged old-field stands of second

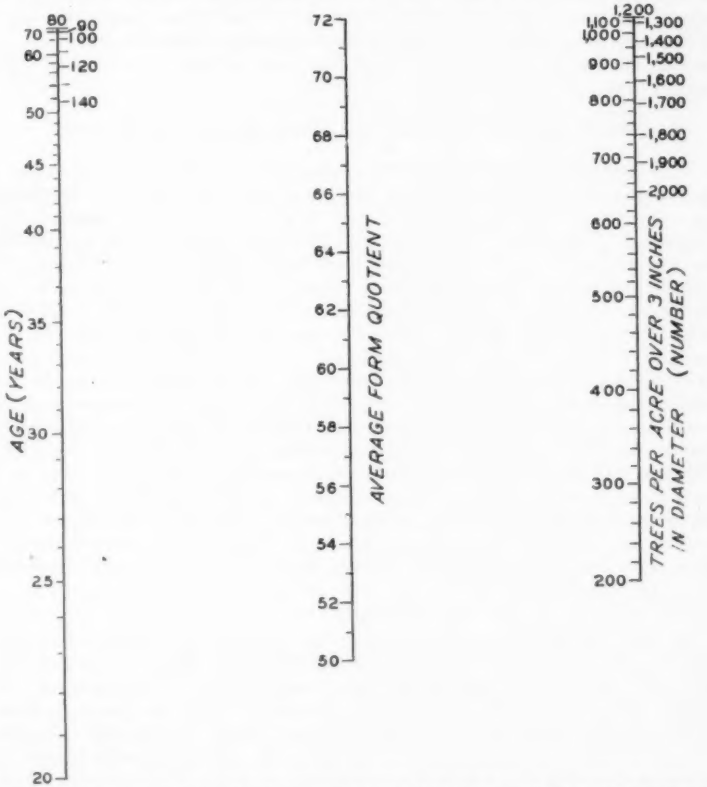

FIGURE 12.—Alinement chart for estimating average form quotient of even-aged stands of balsam fir from age of stand and number of trees per acre over 3 inches d. b. h.

growth. It is most commonly found in pure stands, but when in mixture is more frequently accompanied by balsam fir than red spruce.

Meyer (*8*) observed that red spruce would average considerably shorter in height than either balsam fir or white spruce in even-aged mixtures. When average form quotients are considered it is found that red spruce runs about 4 units of form quotient higher than either white spruce or balsam fir. The difference between red spruce and balsam fir is maintained in old growth as well as in even-aged second

growth, although both species will average higher in form quotient in old growth. Balsam fir and white spruce do not differ appreciably in form quotient when occurring together.

These differences are substantiated by examination of the charts showing the relations between form quotient and form point, crown percent, or diameter, height, and crown percent together. For the range of form points, crown lengths, and sizes most commonly occurring, the red spruce charts will indicate form quotients higher than either balsam fir or white spruce. In the case of charts based on the stand factors (age and number of trees per acre) no appreciable difference is apparent between red spruce and white spruce, although values for balsam fir run lower and appear consistent with the other tests cited.

FACTORS OF BUTT SWELL AND BARK THICKNESS

The accuracy of estimate of standing timber from volume tables is influenced by variations in bark thickness and butt swell of the timber in question as well as by variations in average form quotient. It is important, therefore, to attempt to find out what factors are related to variations in bark thickness and butt swell. This is especially important where basic form-class tables, such as those advocated by the writer, presuppose the elimination of butt swell from the "normal" diameter at breast height. For the use of such tables some basis is needed for reducing actual diameter breast high measurements to normal diameters. But even when the basic taper tables do not assume the elimination of butt swell, it is necessary to reduce outside bark measurements to inside bark diameters, and, since it should prove feasible to combine allowance for butt swell with the bark-thickness reduction, no extra work is involved in the first instance.

In this study an attempt was made to analyze bark thickness and butt swell at breast height independently. Coefficients of multiple correlation were worked out for each of these with diameter, height, form quotient, crown length, crown class, age, number of trees per acre, and site index.

BUTT SWELL

In the case of butt swell only a small proportion of the total variation can be accounted for by these numerical factors, and practically all the variation so accounted for is associated with diameter, the larger trees, of course, having the most butt swell at breast height. Variations in butt swell are much more closely correlated with size in old-growth stands than in second-growth stands, but this might be expected from the fact that the second-growth data were intentionally gathered from stands covering as wide a range of conditions as possible and were, therefore, much more heterogeneous than the old-growth data. Consideration of crown percent or form quotient may slightly improve estimates of butt swell from diameter alone, but this is not clear-cut or consistent in all cases.

The rectilinear alienation coefficients and coefficients of determination brought together in table 13 illustrate the various relationships. Only in the case of old-growth red spruce has it been possible to account for more than 18 percent of the standard deviation of butt swell. Although these coefficients do not represent the full effect of correlation between diameter and butt swell, because definite curva-

ture is present in the case of even-aged white spruce, old-growth red spruce, and old-growth balsam fir, still it is apparent that most of the variance is associated with differences in hereditary characteristics, or with differences in individual situation or anchorage which are not susceptible of numerical evaluation.

TABLE 13.—*Correlation of butt swell at breast height with various factors*

Factors with which butt swell is correlated	Even-aged stands						Old-growth stands			
	Red spruce		White spruce		Balsam fir		Red spruce		Balsam fir	
	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination
All numerical factors	0.85	0.28	0.86	0.26	0.90	0.18	0.63	0.60	0.82	0.33
Diameter breast high alone	.88	.22	.92	.15	.95	.09	.67	.55	.85	.28
Diameter breast high and crown percent	.88	.22	.91	.18	.94	.12	.66	.56	.84	.29
Diameter breast high and form quotient	.88	.23	.92	.15	.94	.12	.67	.55	.83	.31

The amount of butt swell in relation to size of trees is shown in figures 13 and 14. It is about the same in even-aged red spruce and white spruce. The diameter at breast height becomes affected slightly in the 3-inch or 4-inch class, but the amount of butt swell does not exceed 0.2 inch on the average until the trees get beyond the 12-inch class. The amount of butt swell appears to increase sharply for the larger trees, but the data are not strong enough to fix its trend very definitely. In even-aged balsam fir the amount of butt swell in relation to size of trees is only about half of what it is for red and white spruce, and in fact may be almost disregarded as it will seldom exceed 0.1 inch as an average for any of the size classes attained by this species.

The butt swell of old-growth timber is substantially greater than that of even-aged stands for both red spruce and balsam fir. In both cases, starting with trees about 5 inches in diameter, the rate of increase is at first gradual, but becomes quite rapid for trees above 12 inches in diameter. For this size class, butt swell will average about 0.4 inch for red spruce and 0.3 inch for balsam fir. For the 24-inch class the breast-high diameter of old-growth red spruce is enlarged about 2 inches by butt swell.

Some additional points on the behavior of butt swell were obtained by a detailed check of preliminary form-class volume tables prepared from data used in this study. The percentage of total tree volume represented by butt swell as determined by the technic used[10] appears to be fairly constant in trees of all sizes in the case of even-aged white

[10] The difference between total tree volumes, including butt swell, and "normal" volumes was obtained by planimetering charts of cross-sectional areas plotted over height above ground. For the normal volumes, the diameters used were obtained by prolonging the normal convex curve of the main portion of the stem to the ground line as described in Preliminary Calculations (p. 674). For the full volume including butt swell it was necessary to prolong the butt swell by eye down to the 1-foot point, because no measurements had been taken below 2.5 feet aboveground. The stump was considered a cylinder below the 1-foot point.

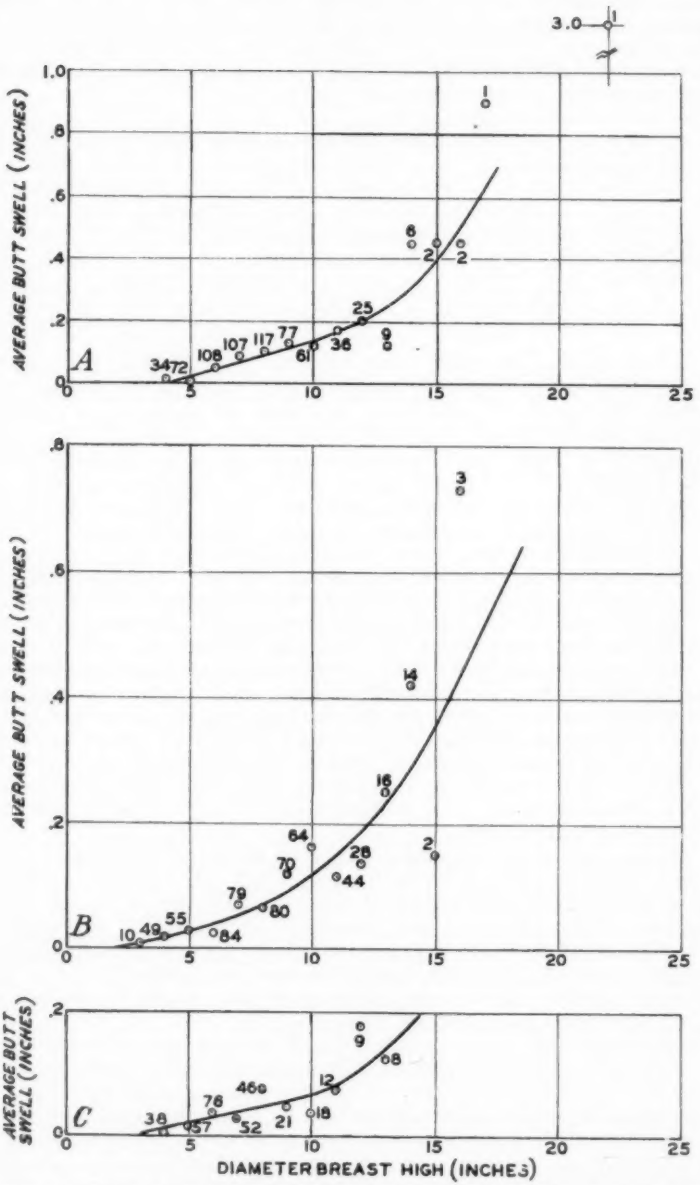

FIGURE 13.—Relation between butt swell and diameter at breast height in even-aged stands: *A*, Red spruce; *B*, white spruce; *C*, balsam fir.

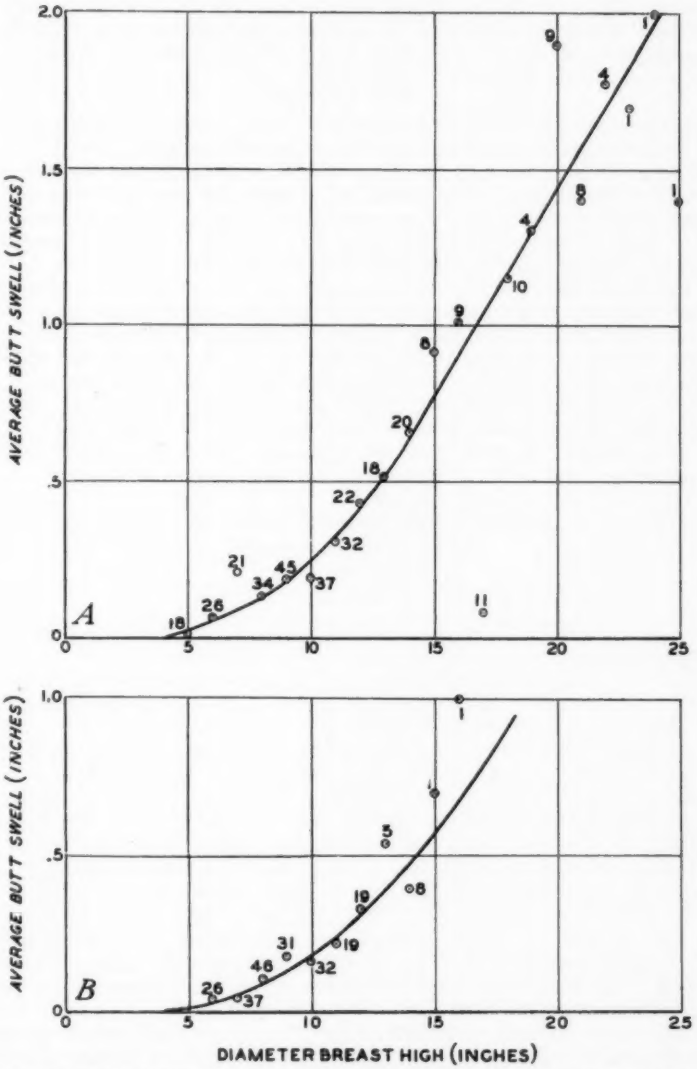

FIGURE 14.—Relation between butt swell and diameter at breast height in old-growth stands: Red *A*, spruce; *B*, balsam fir.

spruce and balsam fir, averaging about 2 percent for the former and 1½ percent for the latter. In the case of even-aged red spruce, however, it increases from 0 for 2-inch trees to 5 percent for 16-inch trees. When analyzed by localities it appears that the percentage of normal volume represented by butt swell decreases as average form quotient of the stand increases, and increases slightly with age.

BARK THICKNESS

When bark thickness is analyzed in similar fashion it is found that a much larger proportion of the total variation is associated with the numerical factors than was the case with butt swell. In the old-growth stands and in the case of even-aged red spruce practically all the variation which can be accounted for is associated with diameter, but with even-aged white spruce and balsam fir there is a substantial margin associated with other measurable factors.

By considering age or site index along with diameter a close approach to the total possible reduction of variation is made in all cases, but the effect of these factors does not appear to be consistent. In the case of white spruce, site index is the most effective factor after diameter, while age has very little influence. On the other hand, in the case of even-aged balsam fir, age accounts for nearly all the possible reduction of variation not associated with diameter.

To indicate the various relationships, a number of rectilinear alienation coefficients are presented in table 14.

TABLE 14.—*Correlation of bark thickness at breast height with various factors*

Factors with which bark thickness is correlated	Even-aged stands						Old-growth stands			
	Red spruce		White spruce		Balsam fir		Red spruce		Balsam fir	
	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination	Alienation coefficient	Coefficient of determination
All numerical factors	0.55	0.70	0.50	0.75	0.54	0.71	0.51	0.74	0.63	0.60
Diameter breast high alone	.58	.66	.62	.62	.76	.42	.55	.70	.66	.56
Diameter breast high and age	.57	.68	.62	.62	.57	.67				
Diameter breast high and site index	.56	.68	.56	.69	.68	.53	.55	.70	.66	.56

The net effect of age on bark thickness is positive, i. e., for trees of a given diameter class the older the tree the thicker the bark. The net effect of site index is generally negative, i. e., other things being equal, trees on better sites will have thinner bark than those on poor sites.

The bark thickness at breast height of even-aged red spruce appears to bear a constant relationship to size, averaging 7 percent of the outside bark diameter. For old-growth red spruce, bark thickness in relation to diameter decreases with increasing size of trees. Up to about 10 inches it is approximately the same as in even-aged stands, tending, however, to be slightly higher than 7 percent for the smaller trees; but it falls off in the larger sizes so that it is only 5.3 percent in

the 24-inch class. This is probably the result of a sloughing off of the scaly outer bark from the old trees more rapidly than new layers are added from within.

In balsam fir the bark thickness in relation to diameter is greater for all sizes in the case of old-growth timber than for even-aged second growth. Unlike that for red spruce, the curve for old-growth balsam fir maintains a constant relation to diameter, while the curve for even-aged second growth falls off slightly with increase in size. This situation is probably due to the difference in bark character of the two species. The smooth bark of balsam fir does not slough off, so a constant relation to size is maintained in the older stands. For old-growth balsam fir, the bark thickness at breast height is maintained at about 5.8 percent of the outside bark diameter for all sizes, while in even-aged stands it drops to about 4 percent for 12-inch trees.

The bark thickness of white spruce is about the same as that of red spruce in the very small size classes, but it becomes relatively less between 5 and 10 inches in diameter and maintains a lower ratio in the larger sizes. It constitutes about 6.3 percent of the diameter breast high in the 6-inch class and 5.2 percent in the 12-inch class.

These relations are illustrated in figures 15 and 16, in which it will be seen that white spruce is about midway between balsam fir and red spruce in respect to bark thickness. By comparison with figures 13 and 14 it is also evident that the amount of butt swell affecting breast-high diameter is never more than half the double bark thickness in trees of these species less than 12 inches in diameter. Butt swell becomes more important than bark thickness only in the case of old-growth red spruce larger than 17 inches d. b. h.

TOTAL REDUCTION OF DIAMETER BREAST HIGH FOR BARK THICKNESS AND BUTT SWELL

Study of each of the factors affecting butt swell and bark thickness having shown that variation in each factor is chiefly associated with variation in diameter breast high, it should be feasible to provide a basis for making allowance for both of these elements together. This should be the most practical procedure, since it is the sum of bark thickness and butt swell at breast height which affects the accuracy of the application of any volume table rather than either of these elements alone.

The relation of total reduction for butt swell and bark thickness to diameter at breast height is shown in figures 17 and 18. It will be seen that there is less curvature than was the case in the plotting of each element separately, because the curvatures of butt swell and bark thickness are in opposite directions and therefore tend to compensate.

The standard errors of estimate from these curves and the corresponding alienation indices and indices of determination are shown in table 15. It appears that the total reduction of breast-high diameter can be estimated from diameter breast high alone, with a standard error not exceeding 0.2 inch in all cases except that of old-growth red spruce, yet the correlation is considerably closer in the case of old-growth red spruce than in any of the other sets of data. Conversely the closest estimate is obtained in the case of even-aged balsam fir where the correlation is lowest.

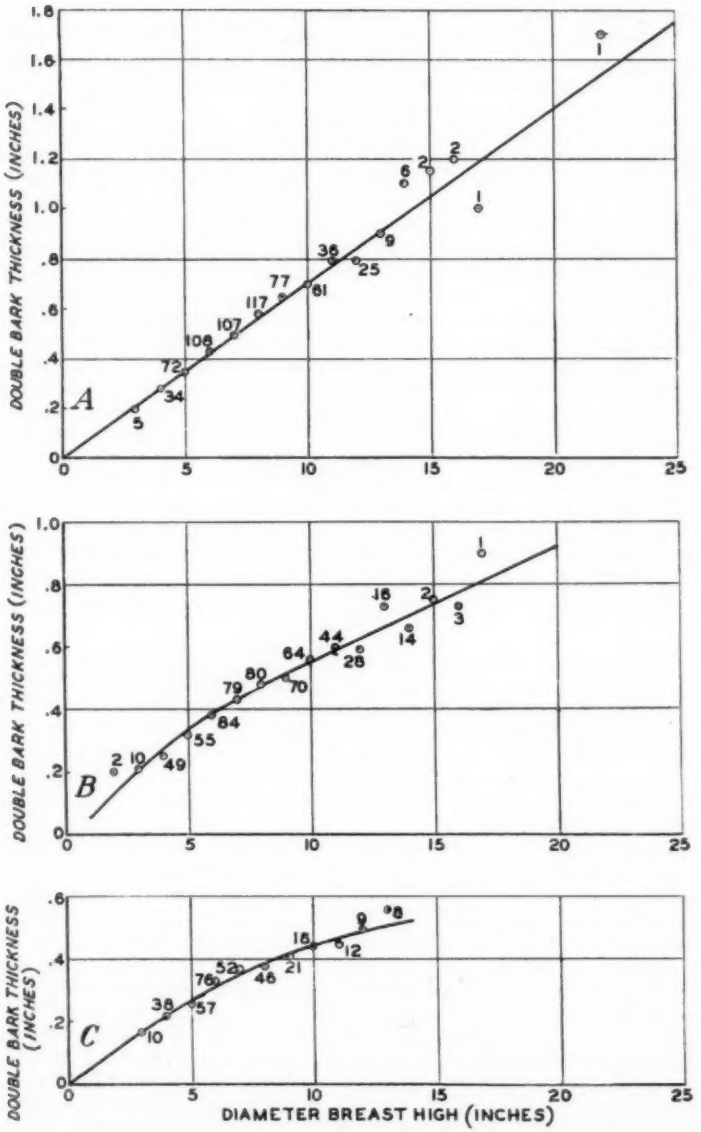

FIGURE 15.—Relation between bark thickness and diameter at breast height in even-aged stands: *A*, Red spruce; *B*, white spruce; *C*, balsam fir.

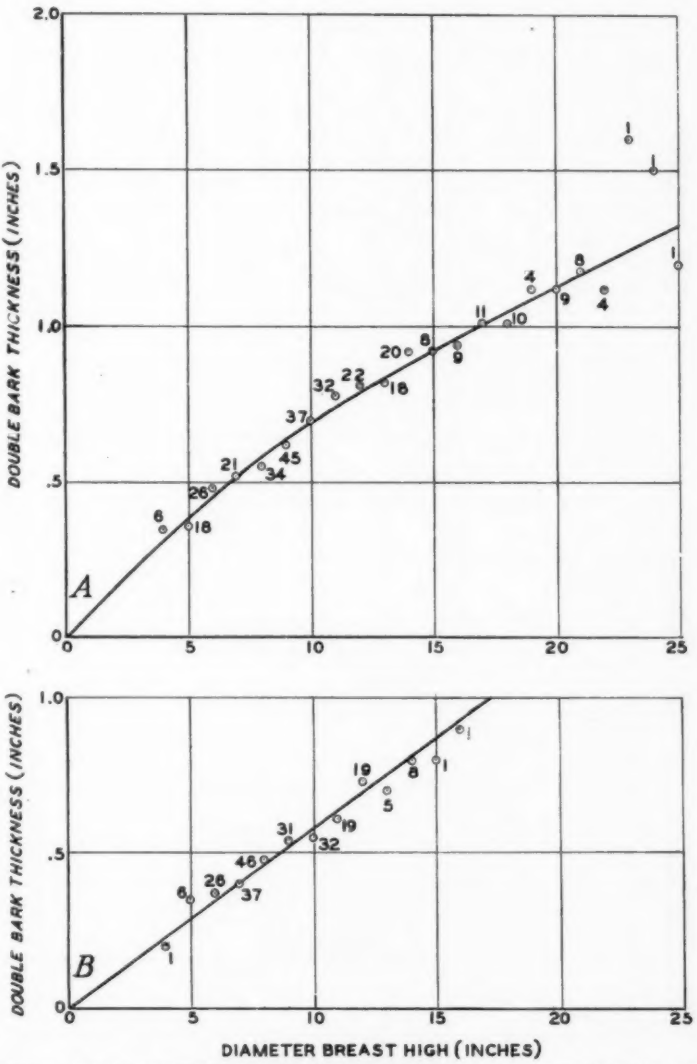

FIGURE 16.—Relation between bark thickness and diameter at breast height in old-growth stands: *A*, Red spruce; *B*, balsam fir.

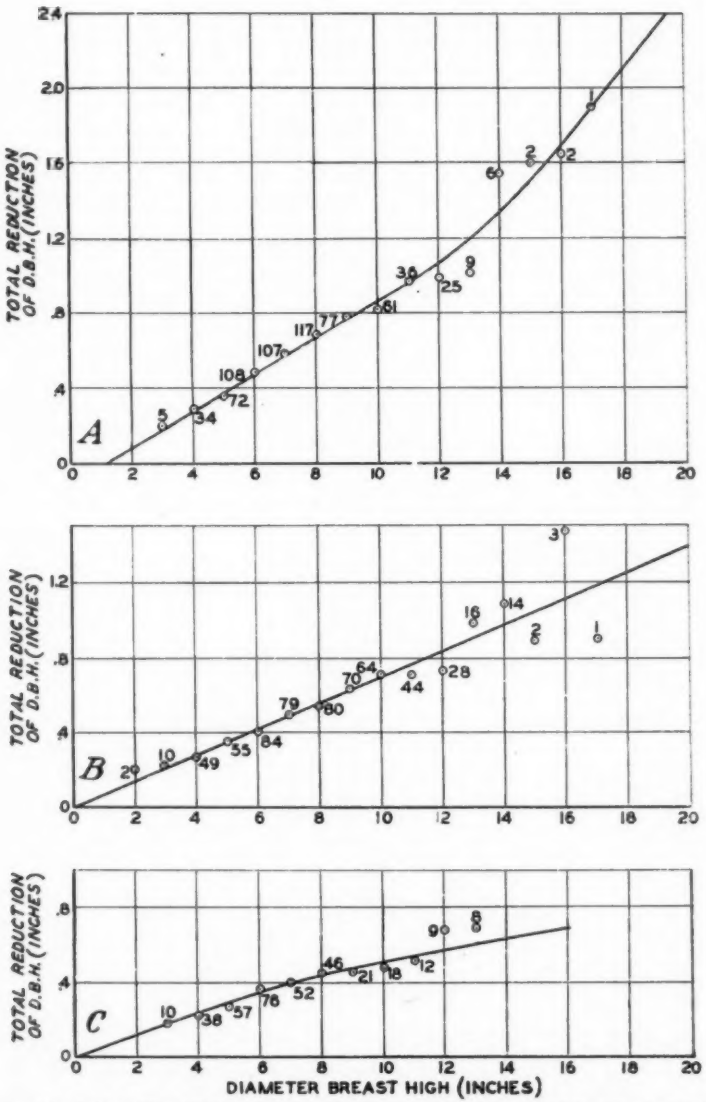

FIGURE 17.—Relation of total reduction of diameter breast high for bark thickness and butt swell to diameter breast high in even-aged stands: *A*, Red spruce; *B*, white spruce; *C*, balsam fir.

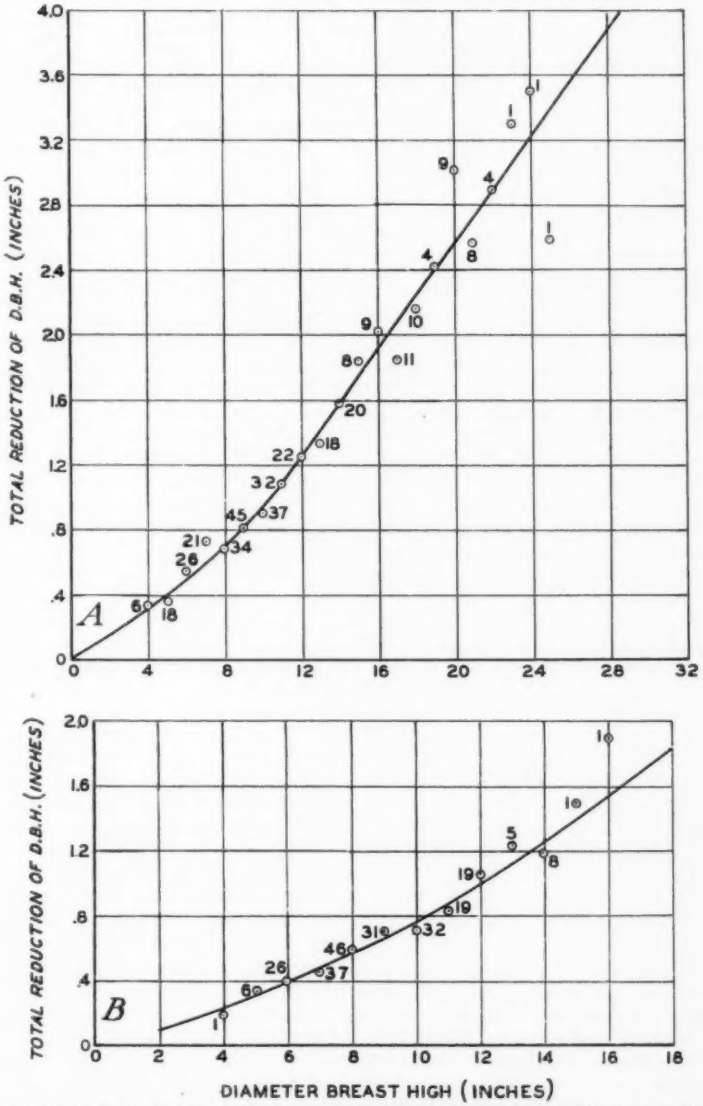

FIGURE 18.—Relation of total reduction of diameter breast high for bark thickness and butt swell to diameter breast high in old-growth stands: *A*, Red spruce; *B*, balsam fir.

TABLE 15.—*Accuracy of estimates of total reduction of diameter breast high for bark thickness and butt swell*

Type and species	Standard deviations of total reductions	Accuracy of estimate of total reduction			Standard error expressed as percentage of mean diameter breast high	Standard error expressed as percentage of volume of individual trees
		Standard error	Alienation index	Index of determination		
Even-aged stands:	*Inches*	*Inches*			*Percent*	*Percent*
Red spruce	0.34	0.20	0.61	0.63	2.6	5.3
White spruce	.27	.19	.71	.50	2.4	4.8
Balsam fir	.17	.14	.80	36	2.0	4.0
Old-growth stands:						
Red spruce	.76	.39	.51	.74	3.5	7.0
Balsam fir	.32	.21	.66	.56	2.4	4.7

Since the influence of other factors was indicated in a general way in the discussion of butt swell and bark thickness, and since so much of the variability that can be accounted for is related to diameter breast high, it seemed desirable here to study the residuals from the curves of total reduction on diameter breast high rather than to use multiple correlation directly.

In the case of even-aged red spruce and white spruce there is a definite tendency for the difference between diameter breast high and normal diameter of trees of the same size class to be greater on poor sites than on good sites. But site index did not show any significant relationship in the old-growth stands or in even-aged balsam fir. Even in the case of even-aged red spruce, where the effect is most pronounced, the accuracy of estimate is increased less than 2 percent (a reduction of the alienation index from 0.61 to 0.59).

For even-aged balsam fir there is a definite relation with age that is not apparent in either of the other species. Balsam fir trees of the same size show a greater difference between diameter breast high and normal diameter in old stands than in younger ones. Trees of the same size would therefore have lower volumes in old stands than in younger ones, provided their form quotients were similar. But since form quotient tends to increase rapidly with age (p. 693) the effect of age on volume is compensating. The improvement of estimate of the total reduction of diameter breast high in even-aged balsam fir when age is taken into consideration amounts to about 16 percent, the alienation index being reduced from 0.80 to 0.64.

The relative significance of variations in bark thickness and butt swell as compared to variation in form quotient can be judged from the effect of each of these elements on estimates of tree and stand volume. Table 16 compares standard errors in tree volumes associated with the estimation of form quotient with those associated with estimates of butt swell and bark thickness. The former are 1.5 times the standard errors in estimation of form quotient from diameter, height, and crown percent (table 11), since a unit of form quotient is roughly equivalent to 1.5 percent of volume. The latter were derived by the approximate method of assuming the standard error expressed as percentage of diameter breast high to be equal to the standard error in inches (table 15) divided by the mean diameter of the trees in the sample, and then multiplying by 2, since it has been previously shown that volume errors will be double the percentage errors in diameter (*2, p. 730*).

TABLE 16.—*Standard errors in estimation of volume of individual trees*

Source of error	Even-aged stands			Old-growth stands	
	Red spruce	White spruce	Balsam fir	Red spruce	Balsam fir
Estimate of form quotient from diameter breast high, height, and crown percent	*Percent* 7.2	*Percent* 6.6	*Percent* 6.2	*Percent* 6.3	*Percent* 6.4
Estimate of butt swell and bark thickness from diameter breast high	5.3	4.8	4.0	7.0	4.7

In the estimation of individual trees variations in butt swell and bark thickness give rise to smaller volume errors than variation in form quotient except in the case of old-growth red spruce. But in interpreting these figures it must be borne in mind that volume tables are used to obtain aggregate volume of groups of trees or of stands and cannot be expected to give great accuracy for individual trees.

The standard error in volume of an entire stand associated with variations in butt swell and bark thickness would be reduced regularly in proportion to the square root of the number of trees tallied. But, if average form quotient is determined by any basis suggested in this paper or by actual measurement of a sample of trees, the standard error associated with variation in form quotient will never be reduced by more than the square root of the number of trees used in such determination, which is not likely to exceed 50.

It therefore appears that the spread between volume errors from these two sources would increase as the number of trees tallied increased. It seems quite certain that with these species, as was found to be the case with ponderosa pine (*2, p. 737*), the determination of average form quotient is a more important source of error than allowance for butt swell and bark thickness, but the latter approaches the former in significance in the larger sized old-growth timber.

CONCLUSIONS

When this study was commenced, it was believed that some adaptation of the form-class system of volume tables as developed in Sweden would prove superior to conventional tables based on diameter and height alone, since form-class tables take definite cognizance of differences in taper. The feasibility of obtaining the theoretical benefits of the form-class system in practice depends upon the soundness of the application of a single average form quotient to the entire stand, and upon ability to estimate the average form quotient satisfactorily and to determine the amount of bark thickness and butt swell. Furthermore, the superiority of tables derived by the form-class system will depend upon the extent to which the determinations of average form quotient and of the reduction of diameter breast high to normal diameter are superior to those that might be made from diameter and height, which are accounted for in tables of the conventional sort.

In this study of red spruce, white spruce, and balsam fir, variations in bark thickness and butt swell could not be consistently correlated with any factor other than diameter. This means that, so far as it will be practical to allow for this element, volume tables of the usual sort would be just as satisfactory as form-class tables.

In the analysis of variations in form quotient, also, diameter and height showed up as the most important factors. To the extent that variations in form quotient are associated with differences in diameter and height, conventional volume tables, if properly constructed and based on truly representative data, will automatically take care of the form-quotient problem. A measure of the superiority of form-class tables in respect to proper allowance for variations in form quotient may be obtained by a comparison of volume errors when form-quotient estimates are based on diameter, height, and crown percent (the most accurate and practical basis for evaluating form quotient developed in this study) with those which arise when form quotient is estimated from diameter and height alone, as is in effect the case with conventional tables. Measures of the accuracy of estimate of form quotient on these two bases are given in the last two lines of table 8, but they will have more meaning if expressed in percentage of volume, as in table 17.

TABLE 17.—*Comparison of volume errors associated with different methods of evaluating form quotient*

Type and species	Standard error in estimating form quotient from diameter breast high, and height[1]	Standard error in estimating form quotient from diameter breast high, height, and crown percent [1]	Improvement [1]
Even-aged stands:	*Percent*	*Percent*	*Percent*
Red spruce	8.3	7.2	1.1
White spruce	7.3	6.6	.7
Balsam fir	6.6	6.2	.4
Old-growth stands:			
Red spruce	7.0	6.3	.7
Balsam fir	7.4	6.4	1.0

[1] Expressed as percentage of volume.

It will be seen that even in this element no practical method of applying the form-class system yet devised offers prospect of giving more than 1 percent greater accuracy than might be expected from conventional tables for the species in question.

It may be argued further that, to the extent that form quotients within stands vary with size of the trees, the form-class system will be less accurate than conventional tables, since in the former a single average form quotient is usually applied to the entire stand whereas in the latter the form quotient varies automatically according to diameter and height.

On the whole, therefore, it may be concluded that in final application the form-class system must be on much the same footing as other volume-table methods, because differences in taper which can be evaluated in any practical way are so largely reflected in the diameter-height relationships. Methods of form-class analysis, however, still offer definite advantages in a more adequate and realistic technic, in reduction of number of trees required for reliable tables, in simplicity of compilation of tables in various units of product or standards of utilization, and in the possibilities for analytical comparison of different species or of timber of the same species under different growth conditions. In the latter field there is the greatest opportunity for future study and progress.

SUMMARY

Intensive study of the variation of form quotients and of bark thickness and butt swell has been undertaken to provide a clearer understanding of factors involved in the application of volume tables, with special reference to the use of the form-class system as developed by the writer in a previous paper. The study is based on measurements of 2,189 trees of red spruce, white spruce, and balsam fir covering a wide range of sizes, ages, densities, sites, and growth conditions in the Northeast. Punch-card machines were used in the manipulation of the data; and methods of multiple curvilinear correlation, as developed by Bruce and Reineke, were used in the analyses.

After graphic elimination of butt swell at breast height, the taper measurements for each locality were found to conform quite satisfactorily to the formula for the stem curve: $\frac{x}{y}=\frac{x}{a+bx}$. Significant volume errors exceeded 2 percent in the case of a few samples only. White spruce gave the best fit. With red spruce the upper sections frequently fell below the formula, especially in old-growth stands. Even-aged balsam fir was similar to red spruce in fit, but in old-growth balsam fir diameters below the midpoint were consistently larger and those above the midpoint consistently smaller than the formula, with the effect on cubic volume tending to compensate.

The standard deviation of form quotients within the stands averaged not far from ± 4.5 units, which conforms to conclusions of previous work; but the variability was not closely associated with any of the factors which can be readily evaluated. However, the variation appeared to decrease with an increase of density, age, or form quotient.

The relation between form point and form quotient differed with each species and was not rectilinear. Although higher form quotients were generally associated with an increase in relative height of form point, very little if any increase in form quotient occurred after the form point went above 75 percent of the total height. In fact, tall trees with crowns of limited development often had relatively low form quotients.

Measurement of form point on about 45 trees is required to limit the standard error of the average form quotient to ± 1 unit. The use of form point has very little significance in old-growth red spruce and balsam fir.

A study of form quotients of the individual trees indicates that more than a third of the total variability of form quotient is associated with factors not included in this study and probably not readily susceptible to numerical evaluation. Of the numerical factors studied, diameter breast high, height, length of crown, and site index were the most important. Diameter and height appeared to have the greatest weight, but, these factors having opposite signs and being closely correlated, their effect was compensating. Form quotient increased rapidly with height until the trees were about 40 feet tall, after which there was little further increase. On the other hand, form quotients were at a maximum in trees about 7 inches in diameter and decreased steadily with increase in diameter. This negative correlation between diameter and form quotient, slight but significant,

appeared within individual stands as well as for the data as a whole. Similarly, within stands, dominant trees averaged lower in form quotient than codominants or intermediates and, as might be expected from this, trees with long crowns had lower form quotients than those with short crowns.

Length of crown is the only factor showing any appreciable crude correlation with form quotient when all the data for each species are thrown together. Form quotients generally reached a maximum in trees with crown lengths about 40 percent of total height. Estimates of form quotient can be made from length of crown with about the same accuracy as from form point.

Although trees on poor sites generally averaged higher in form quotient than those on better sites, the influence of site appeared to be absorbed in the diameter-height-crown length relationships. Alinement charts have been prepared for estimating form quotient of individual trees from diameter, height, and crown percent. Even using these three factors, about 40 trees are required to keep the standard error of the average form quotient down to $\pm$ 1 unit.

The average form quotient of even-aged stands increased rapidly up to an age of 70 years or a density of 1,200 trees per acre more than 3 inches in diameter, but beyond these points, little if any further increase took place. Alinement charts for estimating average form quotient of a stand from its age and density have also been prepared. Just as with individual trees, average form quotient can also be correlated with average crown length of dominant and codominant trees, and there is evidence that variations in average crown length are reflected and expressed approximately by the variations in age and number of trees per acre. For old-growth stands it appears that a single average form quotient may be safely applied upon inspection for certain easily recognized conditions of growth.

Where the species occurred in mixture, red spruce ran about four units of form quotient higher than either white spruce or balsam fir. Balsam fir and white spruce did not differ appreciably in form quotient when occurring together.

The amount of butt swell at breast height tended to increase with increase in diameter, but only a small proportion of the variation of butt swell can be accounted for by analysis of the numerical factors. A larger proportion of the variation in bark thickness can be accounted for, and this too is directly related to diameter. In trees of the species studied less than 12 inches in diameter, butt swell never amounted to more than half the double bark thickness. It exceeded bark thickness only in the case of old-growth red spruce larger than 17 inches diameter breast height.

Butt swell as determined by this study averaged 2 percent of the total tree volume in even-aged white spruce and 1½ percent in even-aged balsam fir, regardless of size, while in even-aged red spruce the percentage of volume increased steadily, reaching 5 percent for trees 16 inches in diameter.

For practical purposes butt swell and bark thickness may be considered together. The total reduction of breast-high diameter can be estimated from diameter breast high alone, with a standard error not exceeding 0.2 inch in all cases except that of old-growth red spruce, yet the correlation is considerably closer in the case of old-growth red spruce than in any of the other sets of data. Although

there is some indication that the difference between diameter breast high and normal diameter is greater on poor sites than on good sites in even-aged red spruce and white spruce, little increase in accuracy of estimate can be obtained from consideration of this factor. In even-aged balsam fir the reduction of diameter breast high to normal diameter is definitely related to age, but the effect this would have on differences in volume for trees of the same size in stands of different ages tends to be offset by the fact that form quotients increase with age.

The determination of average form quotient is clearly shown to be a more important source of error in the estimation of volume of standing timber of the species studied than allowance for butt swell and bark thickness, but the latter approaches the former in significance in the larger sized old-growth timber.

Since so much of the variation in form quotient, bark thickness, and butt swell that can be accounted for is associated with diameter and height, form-class volume tables afford little advantage in actual use over properly constructed tables of conventional form. However, methods of form-class analysis do possess several technical advantages and offer good opportunity for analytical comparison of different species or of timber of the same species under different growth conditions.

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THE RELATIONSHIP OF CERTAIN LEGUME MOSAICS TO BEAN [1]

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INTRODUCTION

Since the virus of the common mosaic disease of bean (*Phaseolus vulgaris* L.) is seed-borne, the disease is widely distributed. Previous investigators (*6*, *11*, *13*)[3] have shown that the amount of seed transmission of the virus varies; primary infected plants seldom produce more than 50 percent of infected seeds, and secondary infected plants produce an even smaller percentage. Notwithstanding the low percentage of seed-borne mosaic in most lots, the disease often becomes so wide-spread in the field, especially among the susceptible varieties, that all the plants may be infected by the end of the growing season.

Common bean mosaic is not equally severe in all sections of the country, which indicates, among other things, that climatic conditions may not be equally favorable for the manifestation of symptoms and that the agencies transferring the virus may be more numerous in some bean-growing sections than in others. There also may be hosts harboring other viruses that may be infectious to beans.

It has frequently been demonstrated and is generally understood that under field conditions the disease is spread by means of aphids from infected to healthy plants, but it has been doubted whether this is the sole source of virus transfer. Field observations have indicated that the source of some of the infection came from mosaic-infected legumes, both cultivated and wild. In some of the irrigated sections of the United States it was repeatedly observed that bean mosaic appeared more severe in the early part of the season along the borders of the field adjacent to fence rows, irrigation ditches, or roadways, which were often overrun with weeds, including several legumes. In a number of instances, 15 to 20 percent of infection was found in the outermost rows whereas only a trace was observed in the center of the field. This difference in severity of infection may have been due either to large aphid populations coming from the weeds transmitting certain of the related legume viruses to bean, or to the spreading of the common bean mosaic from one bean plant to another.

During the course of cross-inoculation studies with virus diseases of certain leguminous hosts it was noted that the virus extracts of some of these diseased hosts when inoculated to the bean produced symptoms unlike those of the common bean mosaic. It was shown that the viruses causing the mosaic diseases of pea (*Pisum sativum* L.), white clover (*Trifolium repens* L.), alsike clover (*T. hybridum* L.), white sweetclover (*Melilotus alba* Desr.), yellow sweetclover (*M. officinalis*

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[3] Reference is made by number (italic) to Literature Cited, p. 748.

(L.) Lam.), alfalfa (*Medicago sativa* L.), and sweet pea (*Lathyrus odoratus* L.) are all transmissible to bean, whereas the virus producing the mosaic of red clover (*Trifolium pratense* L.) is not. Although a careful examination of the symptoms produced by the viruses of these legumes on bean reveals specific differences, the viruses from white clover, white sweetclover, yellow sweetclover, and alsike clover when inoculated to beans may produce under certain conditions symptoms that resemble the typical mottled and chlorotic symptoms of the common bean mosaic.

It is entirely probable that in the several legumes there may be present other mosaic viruses that may react differently from those reported here, notwithstanding symptomatological similarity. Furthermore, viruses from other mosaic-diseased legumes not included here may also produce on beans symptoms different from any so far reported.

In some cases certain viruses were inoculated only to the Stringless Green Refugee variety to determine their infectiousness. The viruses of pea, white clover, white sweetclover, alfalfa, and red clover mosaics were studied in some detail; those of alsike clover, yellow sweetclover, and sweet pea mosaics were not.

This paper describes the symptoms of these legume mosaic diseases on their normal hosts, together with the symptoms produced by these viruses when inoculated to bean, and compares differences in varietal reaction of the several legume mosaic diseases on bean varieties and other leguminous hosts with those of the common bean mosaic. Data on the comparison of the properties of these viruses are also given. An unknown virus obtained from a hybrid bean is compared with the common bean mosaic as to symptomatology and varietal susceptibility and resistance on a number of different bean varieties.

PREVIOUS INVESTIGATIONS

The early literature records few data regarding types or strains of the bean mosaic virus or the transmissibility of other legume mosaic viruses to bean. The early work of Reddick and Stewart (*15, 16, 17, 18*), Pierce and Hungerford (*13*), Fajardo (*6, 7*), and Nelson (*11*) dealt with the common bean mosaic merely as the disease affects the bean plant itself.

Numerous reports of mosaic diseases of other leguminous plants are recorded in the literature. Elliott (*5*) proved the existence of a mosaic disease of sweetclover and red clover and showed the virus to be infectious to these two hosts as well as to *Medicago arabica* (L.) Huds. and *Vicia faba* L. Dickson (*3*) reports successful reciprocal inoculations between the viruses of a number of clover mosaic diseases, but obtained negative results when cross inoculations to pea and bean were made. Carsner (*2*) proved that the virus causing curly top of sugar beets was infectious to beans. Doolittle and Jones (*4*) reported the transmission of a virus of garden pea to red clover and sweet pea. Böning (*1*) described a mosaic disease of broadbean (*Vicia faba*) whose virus was infectious to peas, crimson clover, and red clover. Wingard (*21*) showed that the tobacco ring spot virus was infectious to beans as well as to certain other legumes. Merkel (*10*) attempted to classify the bean mosaic into three types on the basis of symptomatology, and concluded that the mosaic dis-

eases of a number of Leguminosae which he examined were caused by the same virus. Fajardo (*6*) was unable to infect beans with the viruses from certain leguminous hosts and suggested that the mosaic disease of bean is perhaps specific to the bean plant. Price (*14*) showed that the tobacco mosaic virus was infectious to beans, producing local lesions on certain varieties. Weimer (*19, 20*) reported on a mosaic disease of alfalfa and its transmissibility, but did not record any cross-inoculation studies. Nelson (*11*) reported a virus disease of beans as being different from the common bean mosaic, and gave it the name of "rugose" mosaic. Zaumeyer (*22*) and Zaumeyer and Wade (*24*) recently reported on the transmissibility of a number of different legume mosaic diseases to bean and pea and showed that they were not the same as the common bean mosaic. Pierce (*12*) described another virus of bean which he stated is different from the common bean mosaic and which he designated as yellow bean mosaic.

MATERIALS

SOURCES OF VIRUSES

Bean Mosaic

The virus of the common bean mosaic used in the experiments was collected from diseased seedlings of the Stringless Green Refugee, a variety very susceptible to the disease.

Pea Mosaic

One of the pea mosaic viruses was secured from infected Dwarf Telephone peas grown in southeastern Colorado in 1931. The virus extract from such plants when inoculated to bean produces typical and striking systemic mosaic symptoms, which are described later. This disease of pea, although difficult to distinguish on the basis of symptoms from the common pea mosaic, is distinct from it, and for the sake of clarity it will be referred to as pea mosaic virus 2, and that of the common pea mosaic as pea mosaic virus 1. Other pea mosaic material used for comparative purposes was collected in Maryland, Virginia, Montana, California, and Idaho. The lesions produced on beans from the material collected in Maryland were similar to those produced with the Colorado material, while the pea mosaic from the other States was similar to pea mosaic virus 1.

White Clover Mosaic

This virus was secured from material collected in the District of Columbia, Virginia, and Colorado. The reaction of the viruses from these three sources was identical; however, the experimental data presented in this paper are based on the virus from Virginia. The virus extract from this mosaic material produced both systemic and local lesions on certain bean varieties.

Alsike Clover Mosaic

This mosaic material was collected near Rosslyn, Va., in the fall of 1933. Its difference from white clover mosaic was established by the reaction of Robust, Great Northern Idaho No. 1, and Corbett Refugee varieties.

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White Sweetclover Mosaic

Most of the specimens of this mosaic were collected in Maryland, but some were collected in Virginia, Colorado, and Wisconsin.[4] The results obtained from all of these samples were identical.

Yellow Sweetclover Mosaic

This virus was obtained from material collected near Rosslyn, Va., and Greeley, Colo. From the data obtained, it appears that this virus is identical with the virus of white sweetclover mosaic.

Alfalfa Mosaic

The alfalfa mosaic described by Weimer (*19*, *20*) was collected by him and sent to the writers in the fall of 1932. Other mosaic specimens were collected in Virginia and reacted identically with those of Weimer. As reported, this mosaic produces local necrotic lesions on beans. Pierce (*12*) later describes similar lesions produced by an alfalfa virus which he states appears to be distinct from the mosaic on the same species described by Weimer (*19*, *20*).

Red Clover Mosaic

The red clover mosaic virus was collected from diseased plants near Rosslyn, Va. It is believed that this virus is the same as the one described by Doolittle and Jones (*4*) as being infectious to garden peas and sweet peas.

Sweet Pea Mosaic

This virus was extracted from infected plants collected in Colorado. It produced systemic infection when inoculated to beans and appears to be distinct from the mosaic described by Doolittle and Jones (*4*).

Bean Mosaic Virus 3

During the summer of 1932, in the examination of a large number of hybrid bean strains at Greeley, Colo., a very mild mosaic symptom was noted on a few plants of a hybrid in the F_7 generation between the Wells Red Kidney and Stringless Green Refugee varieties, a cross tolerant to the common bean mosaic. This virus produces distinctly different symptoms from those produced by the common bean mosaic on the susceptible bean varieties and is referred to here as bean mosaic virus 3.

SOURCES OF BEANS AND OTHER LEGUMES

The bean varieties used in the experimental work, the results of which are presented in the various tables, came from a number of sources. Many of them were furnished by reputable seed firms and others were grown by the writers. The Stringless Green Refugee used principally in these studies was grown by the writers, either under cloth or carefully rogued for mosaic. Corbett Refugee was furnished by the Sioux City Seed Co. This variety originated from a single plant selection of Stringless Green Refugee and is resistant

[4] From Dr. R. A. Brink, University of Wisconsin, Madison, Wis.

to the common bean mosaic. Great Northern Idaho No. 1 was secured from the Idaho Agricultural Experiment Station. It is also resistant to the bean mosaic and is a selection from the commercial Great Northern bean. The Division of Forage Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, furnished seeds of other leguminous hosts.

METHODS

Previous investigators have reported difficulty in obtaining high percentages of infection with the common bean mosaic virus. Success in transmitting the disease depends on a number of conditions, such as the age of the plant to be inoculated, the age of the infected plant from which the virus is extracted, and the method of applying the inoculum to the plant. An abrasive such as quartz sand in the inoculum used by some other workers was not employed in these experiments because of the severe injury it causes to the inoculated plant. The inoculum was secured by grinding infected leaves in a mortar. When large quantities of the virus were desired, infected plants were passed through a meat grinder before extraction of the virus. The juice was then strained through a piece of cheesecloth and a little of the pulp was enclosed within a small square of cheesecloth and used as a pad for inoculation. In all cases the inoculations were made immediately after extraction, since most of the legume viruses lose their virulence rapidly outside the host.

The small pad saturated in the inoculum was applied to the upper surface of each primary leaf with brisk rubbing. Plants were inoculated when the primary leaves were fully expanded and the trifoliate leaves just unfolding. A block of wood about the size of the leaf to be inoculated was placed under it as a support, and before the block was used a small amount of the inoculum was rubbed on it. By rubbing the upper leaf surface with the pad saturated in the inoculum, the lower surface was slightly injured from the pressure against the supporting block. In this manner the inoculum was applied to both surfaces of the leaf, resulting in a relatively high percentage of infection.

SYMPTOMS

The mosaic disease commonly found on beans produces a large number of variable symptoms depending to a large extent on the variety infected. Even within a variety the symptoms may show decided variations. In such cases symptomatology alone would not be suitable for recognizing the identity of possible strains of the virus. Since the other legume mosaic viruses (pea virus 2, white clover, white sweetclover, alfalfa, and bean virus 3) when inoculated to bean produce symptoms that are distinctly different from the common bean mosaic as well as from one another, they can be separated on a basis of symptoms alone. There is a distinct varietal behavior of these viruses on beans, but the susceptible varieties always produce symptoms typical of the particular virus. Varieties more tolerant to the several viruses produce slightly different symptoms. The susceptibility or resistance to the mosaic viruses reported here of Corbett Refugee, Great Northern Idaho No. 1, and Robust resistant to the common bean mosaic appears to be an important feature in the differentiation of these viruses.

The descriptions of the symptoms produced by the viruses from the five different hosts are based on the symptoms as they occur on the Stringless Green Refugee beans. In a few instances they are described on Corbett Refugee and Robust.

COMMON BEAN MOSAIC

The symptoms of the common bean mosaic are variable, depending somewhat on the variety infected, the age of the plant, and the environmental conditions under which the plants are grown. Affected leaves show, in general, various degrees of mottling and chlorosis, downward cupping of the laminae, which gives an arched appearance to the leaflet, puckering, and blistering (fig. 1). Mosaic-infected leaves may be smaller than healthy ones and very much contorted. Frequently leaves show a darker green area along the midrib and lateral veins (fig. 1, *C* and *H*), together with varying degrees of mottling from only slight to almost complete yellowing (fig. 1, *A*). On the less susceptible varieties a ruffling or crinkling (fig. 1, *B*) of the leaves is characteristic of the disease, and this may be accompanied by a general chlorosis of the leaf with pronounced venation (fig. 1, *C*). Under greenhouse conditions the symptoms on these more tolerant varieties are usually not striking, but under field conditions severe infection may cause a stunting of the plant and reduction in leaf area.

PEA MOSAIC

It has been pointed out that there are at least two distinct forms of pea mosaic. In many respects the symptoms of the two forms are similar to each other and difficult to differentiate, but in other respects they may differ more widely. Both forms appear on the leaves and stipules and are first characterized by a faint mottling, the infected leaves being a lighter green than those of the normal plant. Later the mottling becomes more intense, owing to the presence of numerous dark-green areas, irregular in outline and occurring between the larger veins (fig. 2, *B*, *F*, and *G*).

In pea mosaic virus 2 a pronounced vein clearing appears later, and immediately adjacent to the larger veins the dark-green tissue often persists (fig. 2, *G*). The region between the veins remains green but is of a lighter shade than in the normal healthy plant. Especially along the periphery of the leaves, regions of yellow are often found. The leaves and stipules of the infected plant are smaller than normal, but there is only a slight waving and upward curling of the edges and wrinkling of the leaves. Infected plants are only slightly stunted although the pods may be somewhat malformed and distorted and in some cases reduced in size.

Pea mosaic virus 1 differs from pea mosaic virus 2 in that there is only a slight vein clearing, with streaks of yellow found between the veins (fig. 2, *F*). The infected leaves and stipules are more wrinkled, puckered, and twisted, and smaller in size than those associated with pea mosaic virus 2. In later stages the uppermost leaves become rosetted with the tendrils malformed and knotted (fig. 2, *F*). In pea mosaic virus 2 infection this condition has not been observed. Infected plants are usually more stunted than those infected with pea mosaic virus 2.

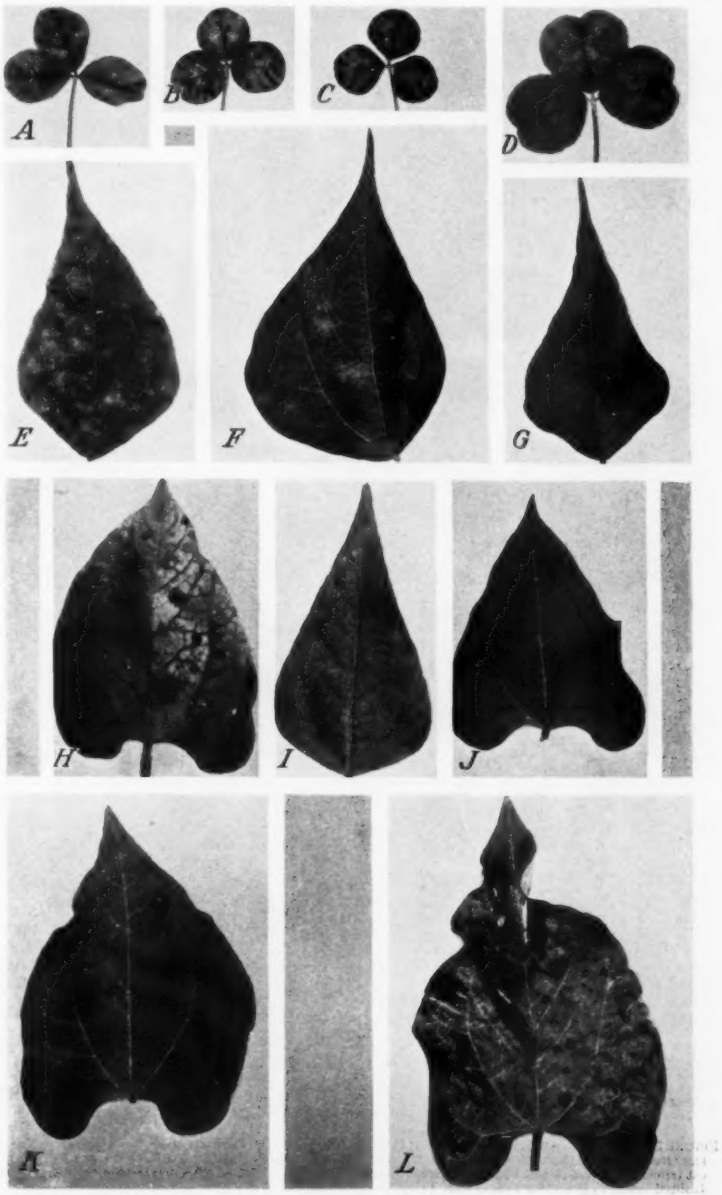

FIGURE 1.—Variations in leaf symptoms of the common bean mosaic on different varieties: *A* and *D*, White-seeded Refugee; *B*, Burpee Stringless Green Pod; *C*, Extra Early Refugee; *E*, Giant Stringless Green Pod; *F*, *H*, and *I*, Stringless Green Refugee; *G*, Refugee Wax.

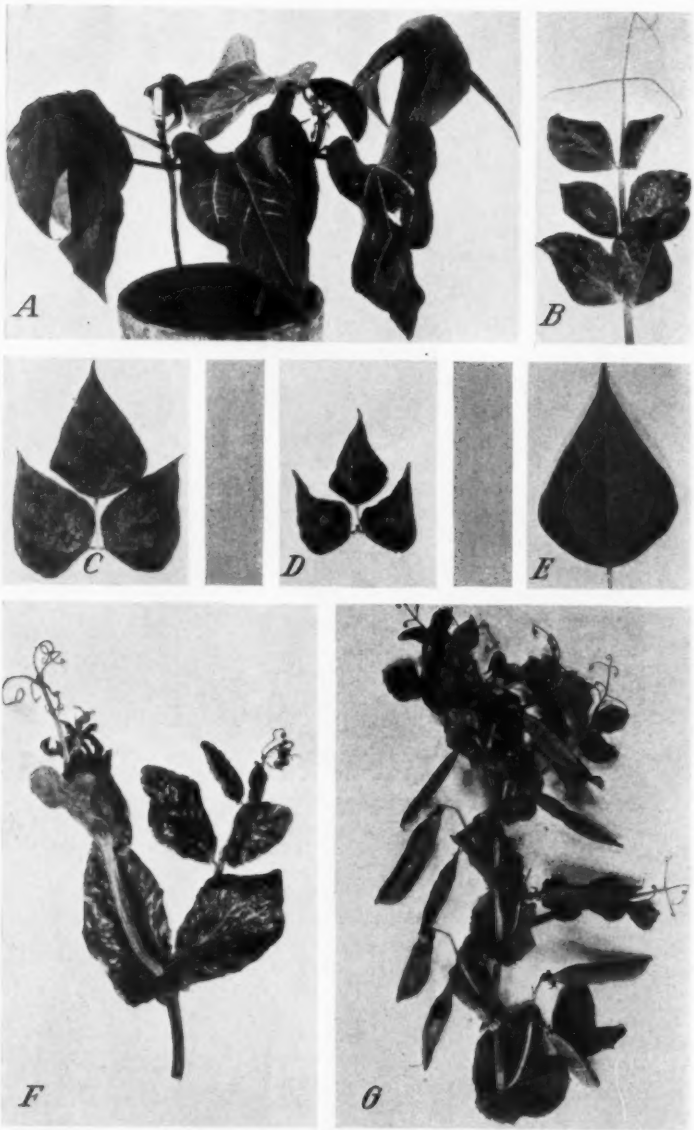

FIGURE 2.—Types of pea mosaic and the symptoms the virus produces when inoculated to beans: *A*, Stringless Green Refugee bean inoculated with pea virus 2; note drooping of leaflets and inward curling of youngest trifoliate leaves; *B*, pea virus 2 on Green Giant pea; *C* and *D*, pea virus 2 on Robust bean; *E*, healthy Robust bean; *F*, pea virus 1 on Dwarf Telephone pea; *G*, pea virus 2 on Dwarf Telephone pea.

PEA VIRUS 2 ON BEANS

The first symptom produced on beans by pea mosaic virus 2 is a drooping of the leaf and leaflets at the pulvini above the point of inoculation (fig. 2, *A*). This symptom is somewhat similar to that produced by the white sweetclover mosaic on beans. Later, numerous small yellow halolike chlorotic spots, varying in size from 1 to 5 mm, develop on these leaflets. The next formed trifoliate leaves appear to be thicker and smaller than the leaves of normal plants, and they droop and curve inward (fig. 2, *A*). Later, chlorotic spots similar to those produced on the first formed trifoliate leaves appear. The growing point of infected plants of susceptible varieties may be killed, and death of the entire plant may follow. Infected plants are usually decidedly stunted and very chlorotic.

Pea mosaic virus 1 was not infectious to beans.

WHITE CLOVER MOSAIC

White clover mosaic first manifests itself on the leaves of white clover as a slight mottle of light- and dark-green areas (fig. 3, *A*, *B*, *C*, and *D*). The darker green regions are usually found adjacent to the main vein and extending outward along the laterals, becoming lighter toward the margin of the leaflet. Occasionally the greater portion of the leaflet may be quite chlorotic with only the basal portion streaked with green. Islands of dark-green areas are frequently found in other portions of the leaf. Infected leaves are usually not distorted, but occasionally there is slight puckering and arching along the main vein. The symptoms are readily masked under certain environmental conditions.

WHITE CLOVER MOSAIC ON BEAN

When the white clover mosaic virus is inoculated to beans, it produces both local necrotic lesions and a systemic infection (fig. 3). Whether both symptoms are produced by the same virus or by two viruses has not been determined. The local lesions may appear from 36 to 48 hours after inoculation as small, somewhat circular, light-green areas, which at times may attain a diameter of from 2.5 to 5 mm (fig. 3, *H* and *L*). The smaller spots are circular with their edges only slightly irregular, whereas the large spots are seldom circular but are very irregular in outline. Later the lesions become brownish red, often accompanied by a slight clearing in the center which is usually surrounded by a dark ring of tissue, while outside of this is a region of lighter brown to red tissue. When the spots are very large with irregular borders there is no marked zonation of the lesions. If the lesions are numerous the uninfected normal green portions of the leaf turn yellow and die.

The systemic infection usually appears 10 to 11 days after inoculation and is manifested by blotches of light green or yellow areas on the trifoliate leaves, irregular in outline (fig. 3, *E*, *F*, and *G*). They are not bounded by the veins but extend throughout any portion of the lamina. These blotched areas may coalesce with similar areas, in some cases covering three-quarters of the leaf surface (fig. 3, *G*), leaving only small islands of normal green tissue. The infected leaves may show a slight ruffling, but their size is not reduced nor is

the leaf malformed as is often found with the common bean mosaic. Infected plants are not stunted, and under greenhouse conditions the

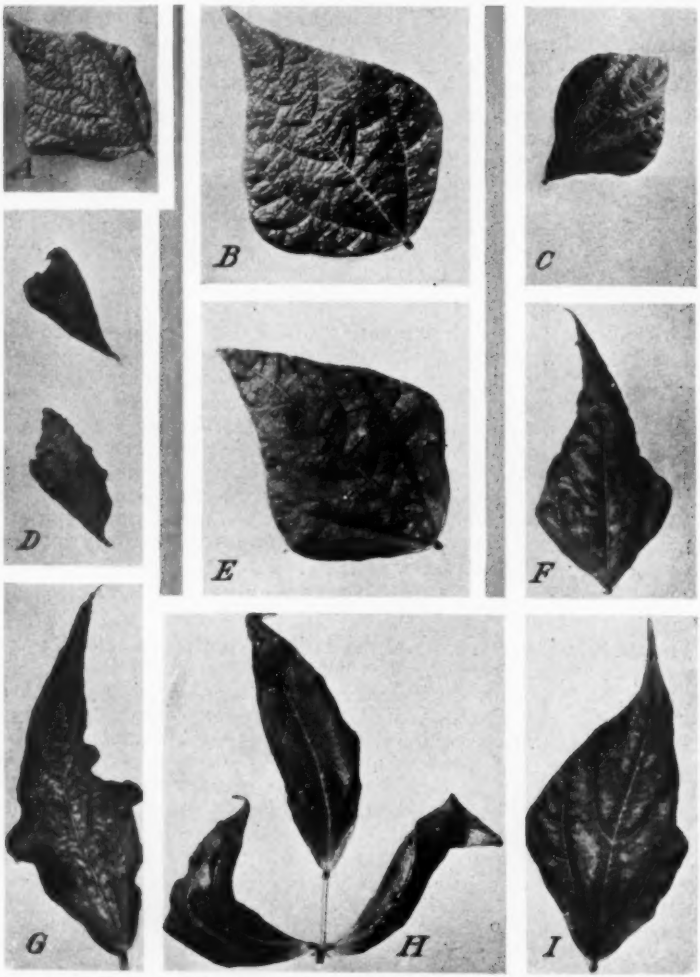

FIGURE 3.—White clover mosaic and the systemic and local symptoms the virus produces on different bean varieties: *A*, *B*, *C*, and *D*, White clover; *E*, trifoliate leaflet of Davis White Wax bean showing mottling; *F*, Pencil Pod Black Wax bean; *G*, Stringless Green Refugee bean; *H*, local lesions on Robust bean; *I* and *K*, healthy Stringless Green Refugee bean; *J*, healthy Robust bean; *L*, local lesions on Stringless Green Refugee bean.

symptoms may be readily masked. Under field conditions the symptoms might readily be mistaken for mild infections of the bean mosaic.

WHITE SWEETCLOVER MOSAIC

The symptoms of white sweetclover mosaic first appear as small light-yellow spots on the leaves (fig. 4, *F* and *G*). These spots may enlarge and coalesce with others, producing small light-green blotches interspersed with dark-green areas (fig. 4, *E*). Frequently there is a clearing of the veins, with the dark-green islands located between them. Severe infection may cause slight dwarfing and ruffling of the leaves. Under field conditions the infected plant may show a stunting in the early part of the year, but later in the summer and under high temperatures the symptoms become masked and the plant may be normal in size.

WHITE SWEETCLOVER MOSAIC ON BEAN

The white sweetclover mosaic virus produces very distinctive symptoms on beans. The first symptom appears about 1 week after inoculation and is a drooping of the leaf and leaflets at the pulvini. Later, small yellow, halolike chlorotic spots varying in size from 1.0 to 3.0 mm in diameter appear on these as well as on later formed leaves (fig. 4, *I*). The spots may be so numerous that they almost cover an entire leaflet and upon coalescing produce a pronounced chlorotic condition (fig. 4, *A* and *H*). Older leaves become roughened and chlorotic. Infected leaves may be stunted and distorted, especially if the infection is localized in one-half of the leaf (fig. 4, *B*). The diseased plants are smaller than the normal ones, but in no case has death resulted from infection.

ALFALFA MOSAIC

Alfalfa mosaic is first noticeable as small greenish or light-yellow streaks either along or between the veins (fig. 5, *B*, *C*, *D*, *E*, *F*, and *G*). These areas gradually become larger and the light areas more nearly yellow. In some cases only a portion of a leaflet may show symptoms. Such regions are usually bounded by a very irregular or jagged border of yellow, while the region within is lighter yellow in color. These areas may be either within the lamina or along the periphery of the leaflet. Oftentimes only 1 or 2 leaflets may show these symptoms, the third being normal in appearance. Another symptom that is found occasionally is manifested by concentric regions of yellow and green (fig. 5, *C* and *E*) which resemble the work done by the insect leaf miner.

ALFALFA MOSAIC ON BEANS

When inoculated to beans, the alfalfa mosaic virus produces small, reddish-brown, local lesions 2 days after inoculation (fig. 5, *A*). Some of the spots are surrounded by an irregular ring of tiny lesions of the same color. The larger type lesions vary from 0.5 to 2.0 mm in diameter. With age, the irregular ring of small lesions coalesces with the larger one and a clearing occurs in the center. The lesions differ from those produced by the white clover mosaic in that they are smaller in size and their edges are more regular. The disease does not become systemic.

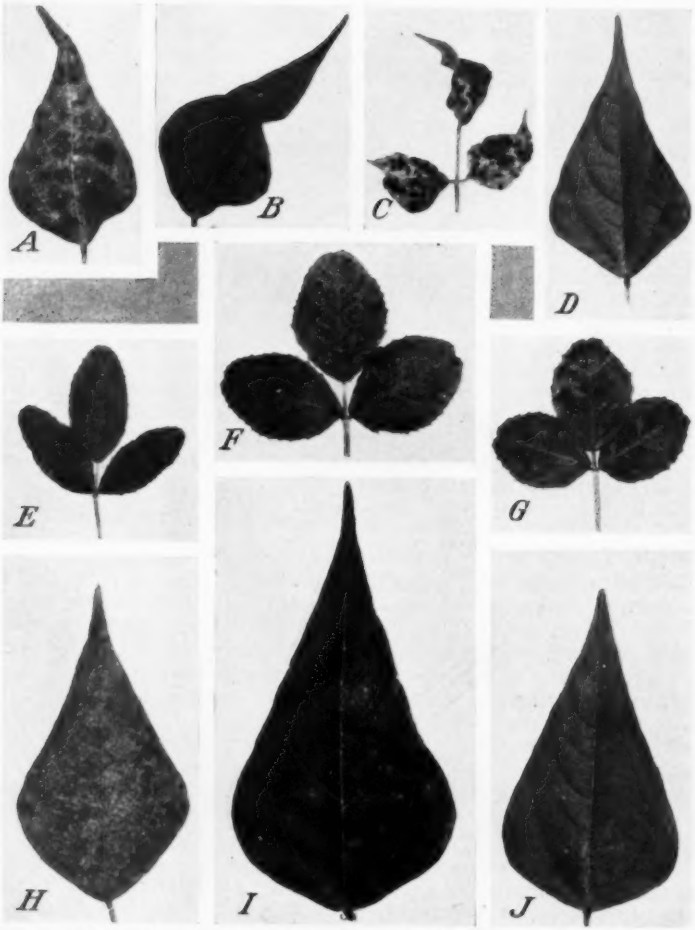

FIGURE 4.—White sweetclover mosaic and the symptoms produced by the virus on different bean varieties: *A*, Corbett Refugee bean showing mottling; *B*, Stringless Green Refugee bean showing distortion of leaflet; *C*, Blue Lake bean showing malformation; *D*, healthy Corbett Refugee bean; *E*, *F*, and *G*, different patterns of white sweetclover mosaic; *H* and *I*, Stringless Green Refugee bean; *J*, healthy Stringless Green Refugee bean.

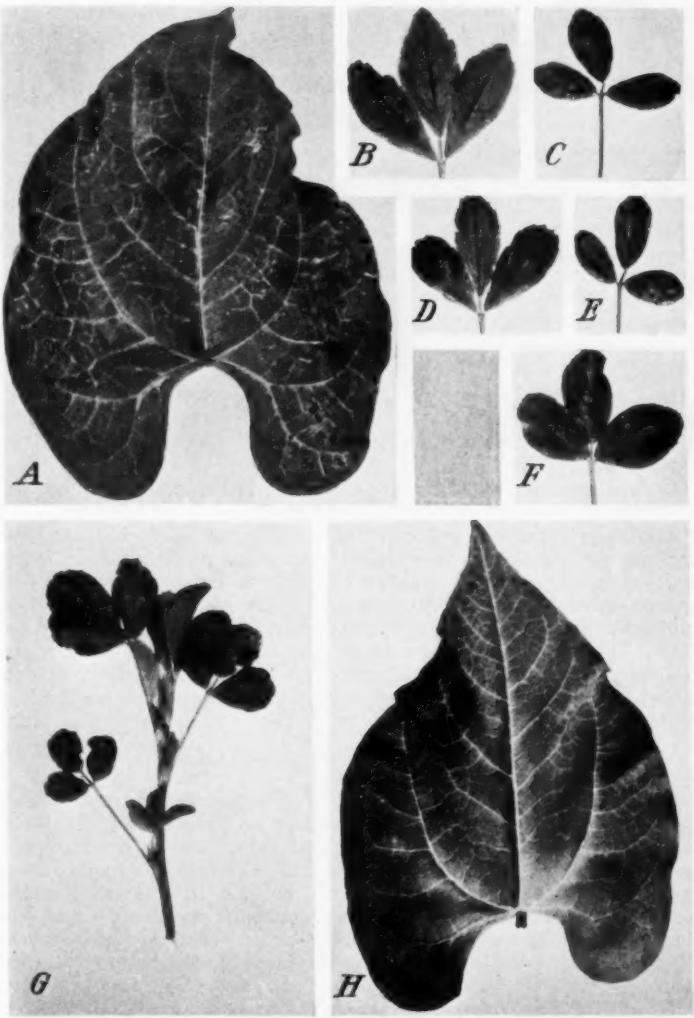

FIGURE 5.—Symptoms of alfalfa mosaic: *A*, Local lesions on bean (Stringless Green Refugee) produced by the virus of alfalfa mosaic; *B*, *C*, *D*, *E*, *F*, and *G*, different patterns of alfalfa mosaic; *H*, healthy Stringless Green Refugee bean.

RED CLOVER MOSAIC

Red clover mosaic appears as a faint mottling and yellow streaking of the leaves (fig. 6, *B*). The yellowing may cover a considerable portion of the leaf, leaving only islands of green which are frequently located adjacent to the veins. Infected plants are seldom stunted, and the symptoms are readily masked under conditions of high temperature.

Red clover mosaic was not infectious to beans.

RED CLOVER MOSAIC ON LEGUMES OTHER THAN BEANS

The leaflets of sweet peas infected with red clover mosaic show a pronounced mottling, pocking, and inward curling and occasionally some streaking. When the infection extends to the flowers there is a decided streaking, curling of the petals, and in many cases stunting.

Infected peas show a distinct mottling on the leaves and stipules very much like pea mosaic 1 and 2 (fig. 6, *F*.)

On the broadbean (*Vicia faba* L.) the infection is manifested by a very pronounced mottling and streaking of the leaves (fig. 6, *E*).

BEAN MOSAIC 3

Bean mosaic 3 appears as a very mild chlorosis on the hybrid of Stringless Green Refugee × Wells Red Kidney. The symptoms might be overlooked, as no malformation of the leaves and no stunting of the plant are produced.

On Stringless Green Refugee bean the first symptoms produced by bean mosaic virus 3, 10 days after inoculation, are characterized by an extremely chlorotic and dwarfed condition of the trifoliate leaves immediately above the inoculated ones (fig. 7, *B*). Later formed leaves may show a very marked clearing of the veins and veinlets, bordered with normal green tissue. Later the remainder of the interveinal tissue turns yellow, resembling in general effect a calico pattern (fig. 7, *A*). The leaves of diseased plants are smaller than those of normal plants, but there is no wrinkling, curling, or other malformation. Infected plants of susceptible varieties may show a decided stunting.

RESISTANCE AND SUSCEPTIBILITY

Studies of previous workers (*6*, *13*, *15*, *16*) on varietal resistance and susceptibility to the common bean mosaic virus, as well as the results obtained by the writers in these experiments, have shown that most bean varieties are susceptible but that they vary considerably in the degree of infection. Corbett Refugee, Robust, and Great Northern Idaho No. 1 were the only resistant varieties used that had been previously demonstrated to be immune to the common bean mosaic.

Transmission of the mosaic viruses of pea, white clover, white sweetclover, alfalfa, and bean mosaic virus 3 suggested the transmission to other varieties of beans to learn whether the behavior toward these mosaic diseases differed from that toward the common bean mosaic. Thirty varieties were inoculated under greenhouse conditions. Plants for this test were grown in greenhouse benches and inoculated, in the manner described previously, with an undiluted virus extract from the various mosaics, when the compound leaves

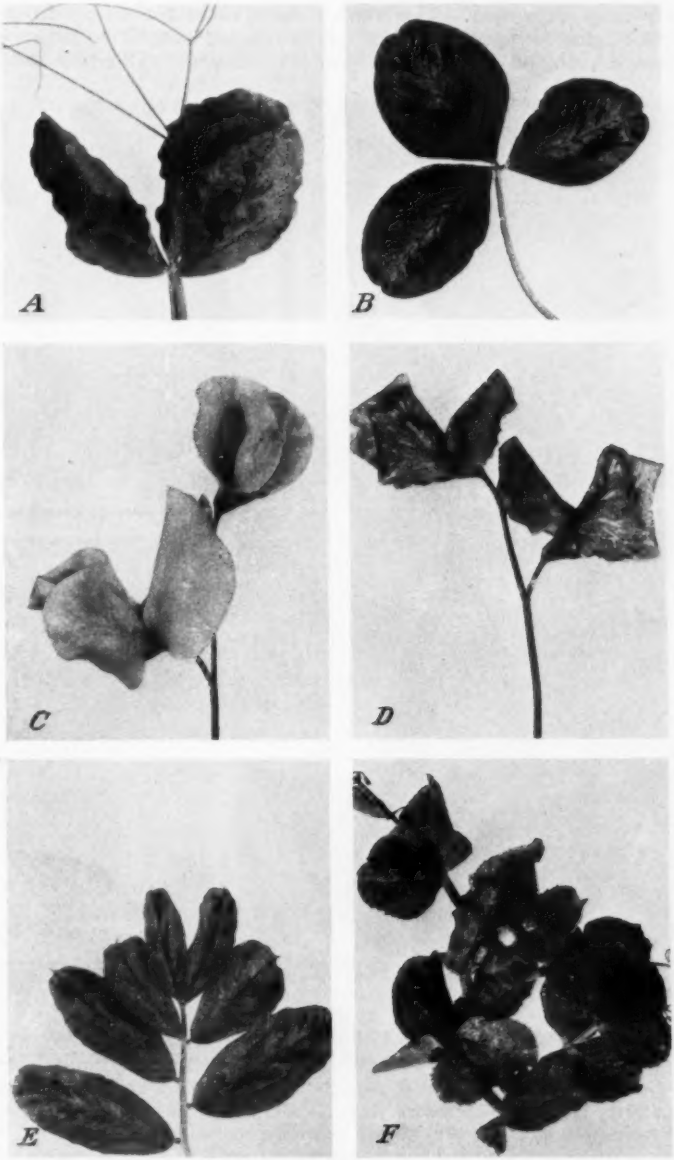

FIGURE 6.—Red clover mosaic and the symptoms produced by the virus on sweet pea, broadbean, and pea: *A*, Leaflets of sweet pea showing mottling; *B*, red clover mosaic; *C*, healthy sweet pea flowers (Baltimore Rose variety); *D*, infected sweet pea flowers showing streaking; *E*, broadbean showing mottling; *F*, pea (Dwarf Telephone variety) showing mottling.

were fully expanded. The viruses were extracted either from the mosaic-affected tissues of the original host plant or from beans infected with the several legume mosaic diseases. In either case the

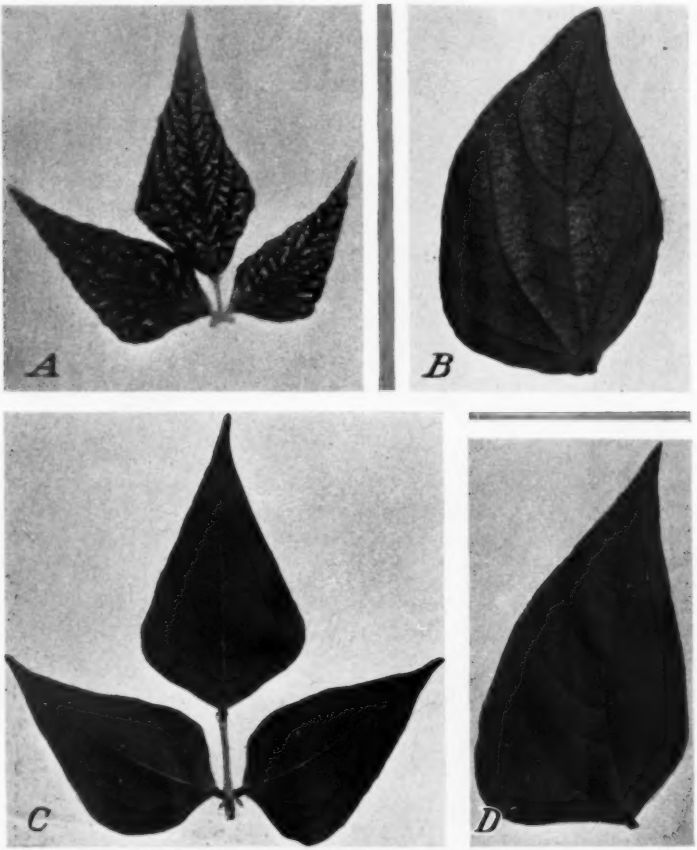

FIGURE 7.—Symptoms of bean mosaic virus 3 on Stringless Green Refugee bean: *A*, Trifoliate leaves showing extreme yellowing between the veins; *B*, leaf showing slight chlorosis; *C* and *D*, leaves from uninoculated plant.

results were comparable. The varieties listed in table 1 were not all grown and inoculated at the same time but were run in four series.

TABLE 1.—*Comparative results of susceptibility and resistance of bean varieties to mosaic viruses of bean, pea, white clover, white sweetclover, alfalfa, and red clover, grouped according to susceptibility to the common bean mosaic*

Group and variety	Results of inoculation with virus indicated [1]													
	Bean mosaic		Pea mosaic 2		White clover mosaic				White sweetclover mosaic		Alfalfa mosaic, local lesions		Red clover mosaic	
					Systemic lesions		Local lesions							
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected
Group 1, very susceptible:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Dwarf Horticultural	10	10*b*	10	4*a*, 6*b*	10	5*c*	19	1	12	9*c*	10	10	8	0
Extra Early Red Valentine	10	8*b*	13	1*a*, 12*b*	18	8*b*, 2*c*	18	3	12	10*c*	9	7	10	0
Red Valentine	10	9*b*	10	1*a*, 4*b*	17	8*b*, 3*c*	18	7	10	8*c*	10	10	7	0
Refugee 1000-1	10	10*b*	10	10*a*	10	8*b*	10	8	12	9*b*	10	10	9	0
Refugee Wax	11	9*b*	10	5*a*, 5*b*	14	7*b*, 2*c*	14	0	10	9*c*	10	10	10	0
Stringless Green Refugee	15	15*b*	19	10*a*, 9*b*	24	23*b*	24	24	20	19*b*	10	10	15	0
Early Stringless Refugee	12	12*b*	10	10*a*	11	9*b*	11	7	10	8*b*	9	9	7	0
Group 2, moderately susceptible:														
Black Valentine	15	12*c*	17	6*a*, 11*b*	20	2*b*, 14*c*	20	0	11	5*c*	10	6	8	0
Blue Lake	10	10*c*	9	3*a*	19	4*b*, 1*c*	19	2	18	1*c*	10	10	7	0
Bountiful	9	9*c*	13	6*a*, 7*b*	16	5*b*, 11*c*	17	5	14	10*c*	10	10	9	0
Burpee Stringless Green Pod	12	11*c*	13	4*a*, 9*b*	16	8*b*, 4*c*	16	3	10	5*c*	9	8	10	0
Brittle Wax	13	12*c*	12	2*a*, 10*b*	16	12*c*	16	7	10	5*c*	10	10	10	0
California White	10	4*c*	9	3*a*	10	5*b*	----	----	10	0	10	10	8	0
Davis White Wax	10	10*c*	9	9*b*	15	7*b*, 7*c*	15	2	10	10*c*	10	7	9	0
French Horticultural	14	11*c*	12	8*b*, 4*c*	20	7*b*, 3*c*	20	5	14	12*c*	10	10	10	0
Full Measure	13	11*c*	10	2*a*, 8*b*	19	12*b*, 6*c*	19	11	10	8*c*	10	8	7	0
Giant Stringless Green Pod	12	11*c*	15	8*b*, 7*c*	17	14*b*, 1*c*	18	8	10	7*c*	10	10	9	0
Konserva	10	5*c*	16	2*a*, 6*b*	17	10*c*	17	4	14	7*c*	8	0	7	0
Longfellow	15	14*c*	11	2*a*, 9*b*	17	12*b*, 5*c*	17	3	14	10*c*	10	8	8	0
Low Champion Bush	14	11*c*	12	5*a*, 7*b*	17	11*c*	17	6	14	8*c*	10	10	10	0
New Stringless Green Pod	10	9*c*	13	2*a*, 11*b*	15	13*b*, 1*c*	15	4	10	5*c*	10	10	10	0
Pencil Pod Black Wax	14	13*c*	12	2*a*, 10*b*	19	12*b*, 4*c*	19	10	9	6*c*	10	10	8	0
Red Kidney (Dark Mahogany strain)	11	7*c*	13	2*a*, 6*b*	18	0	21	9	20	0	8	8	6	0
Stringless Kidney Wax	10	9*c*	17	6*a*, 9*b*	20	3*b*, 3*c*	20	4	10	2*c*	9	9	8	0
Sure Crop Wax	10	9*c*	14	7*b*, 7*c*	13	8*b*	19	11	18	3*c*	10	10	7	0
Tendergreen	10	10*c*	10	7*a*, 3*b*	17	4*b*, 12*c*	15	7	10	9*c*	10	10	10	0
Tennessee Green Pod	10	10*c*	12	6*a*, 1*b*	17	4*b*, 1*c*	20	6	11	1*c*	7	2	10	0
Unrivalled Wax	13	2*c*	12	9*c*	18	6*c*	19	6	14	3*c*	14	6	9	0
Group 3, resistant:														
Corbett Refugee	15	0	15	3*a*, 12*b*	31	4*b*, 15*c*	31	0	35	4*c*	10	0	10	0
Great Northern Idaho No. 1	10	0	16	0	18	0	26	0	12	0	10	3	9	0
Robust	10	0	12	2*a*, 8*b*	22	7*c*	23	3	30	0	13	3	10	0

[1] *a* represents death of plant, *b* serious infection, *c* mild infection.

COMMON BEAN MOSAIC

In table 1 the varieties are grouped according to their relative susceptibility to the common bean mosaic. The 7 varieties in the first group are very susceptible; the 21 in the next group are moderately susceptible; and the 3 in the last group are resistant. It can be seen that in most cases a fairly high percentage of inoculated plants became infected in group 2 of the moderately susceptible varieties. But the symptoms produced were mild, whereas those in the first group (very susceptible) were severe. Under field conditions most varieties in the second group would not show a high percentage of infection and little if any stunting or reduced yield, while in the first group most of the varieties, especially the Refugee types, under ideal conditions and in some localities would show high percentages of disease with considerable stunting and reduced yield.

PEA MOSAIC VIRUS 2

All varieties of beans except Great Northern Idaho No. 1 were infected with pea mosaic virus 2 (table 1). In most of the inoculated varieties a percentage of the plants manifested severe symptoms and were killed. In the case of Refugee 1000–1 and Early Stringless Refugee all of the inoculated plants died. In group 1 there appears to be a correlation between the susceptibility of the different varieties to the pea mosaic virus 2 and to the common bean mosaic, because 100 percent infection was observed in practically all varieties except Red Valentine. In group 2 this correlation is not so evident. A very high percentage of infection occurred with the production of severe symptoms except in the case of Unrivalled Wax. This variety was the only one in this group that showed mild symptoms. Great Northern Idaho No. 1, which is resistant to the viruses of both the common bean mosaic and pea mosaic 2, offered the only point of similarity in group 3. The Corbett Refugee and Robust varieties showed extreme susceptibility to pea mosaic virus 2.

WHITE CLOVER MOSAIC VIRUS

Thirty-one varieties of beans were inoculated with the white clover mosaic virus, and only the Great Northern Idaho No. 1 was resistant. The Red Kidney (Dark Mahogany strain) alone showed only local lesions, with no systemic infection. Twenty-two varieties manifested very marked symptoms, while 6 varieties were only slightly infected. In addition to the mottled mosaic symptoms produced on the susceptible varieties, local lesions were produced on 25 varieties. The varieties resistant to the local lesions were Refugee Wax, Black Valentine, Corbett Refugee, and Great Northern Idaho No. 1.

In group 1 all the varieties showed very marked symptoms of the systemic infection except Dwarf Horticultural, which was only mildly infected. In group 2 Red Kidney (Dark Mahogany strain) was resistant to the systemic infection but susceptible to the local lesions. Although the percentage of infection was quite high in most cases, the symptoms produced were severe in 16 varieties and mild in 4. In group 3 Great Northern Idaho No. 1 was resistant, while Corbett Refugee and Robust were susceptible, the latter variety being less susceptible than the former. Regarding the production of local lesions, all varieties in group 1 were susceptible except Refugee Wax. Dwarf Horticultural and Extra Early Red Valentine were only mildly infected. In group 2 only Black Valentine was resistant, while the other varieties were only mildly susceptible. In group 3 Corbett Refugee and Great Northern Idaho No. 1 were resistant, while Robust was susceptible to the local lesions. There appears to be no complete correlation between the systemic and the local lesions produced by the white clover mosaic virus on beans.

WHITE SWEETCLOVER MOSAIC VIRUS

The white sweetclover mosaic virus infected 27 out of 31 varieties. The 4 resistant varieties were California White, Red Kidney (Dark Mahogany strain), Great Northern Idaho No. 1, and Robust. Three varieties were severely infected, while 24 showed milder symptoms. All the severely infected varieties were of the Refugee type found in

group 1. Refugee Wax, however, was mildly infected. In group 2 most of the varieties were mildly infected. Although many of the varieties in group 1 showed mild symptoms, a high percentage of the inoculated plants became infected. In group 2 most of the varieties showed lower percentages of infection in addition to the weak symptoms produced. In group 3 the only susceptible variety was the Corbett Refugee.

ALFALFA MOSAIC VIRUS

Alfalfa mosaic virus was infectious to all varieties except Corbett Refugee and Konserva. It produced only local lesions.

BEAN MOSAIC 3

The data in table 2 show that in general the mosaic virus from the hybrid bean produces more severe symptoms on beans than does the common bean mosaic. There appears to be no correlation between this virus (bean mosaic 3) and the one causing the common mosaic of beans. Two varieties (Great Northern Idaho No. 1 and Robust) that are resistant to bean mosaic were also resistant to bean mosaic 3,

TABLE 2.—*Comparative susceptibility and resistance of bean varieties to the viruses of the common bean mosaic and bean mosaic 3, grouped according to the susceptibility to the common bean mosaic*

Group and variety	Results of inoculation with virus indicated [1]			
	Common bean mosaic		Bean mosaic 3	
	Plants inoculated	Plants infected	Plants inoculated	Plants infected
	Number	*Number*	*Number*	*Number*
Group 1, very susceptible:				
Dwarf Horticultural	10	10*b*	12	8*c*
Red Valentine (Extra Early)	10	8*b*	10	5*c*
Red Valentine	10	9*b*	10	0
Refugee 1000-1	10	10*b*	10	7*b*
Refugee Wax	11	9*b*	9	8*b*
Stringless Green Refugee	15	15*b*	10	8*b*
Stringless Refugee (Early)	12	12*b*	8	6*b*
White Seeded Refugee	10	10*b*	10	6*b*
Group 2, moderately susceptible:				
Black Valentine	15	12*c*	9	4*c*
Blue Lake	9	3*c*	10	0
Bountiful	9	9*c*	10	10*b*
Burpee Stringless Green Pod	12	11*c*	10	10*b*
Brittle Wax	13	12*c*	10	4*c*
California White	10	4*c*	10	0
Davis White Wax	10	10*c*	10	10*b*
French Horticultural	14	11*c*	10	2*b*
Full Measure	13	11*c*	9	5*c*
Giant Stringless Green Pod	12	11*c*	10	10*b*
Konserva	10	5*c*	9	0
Longfellow	15	14*c*	9	7*c*
Low Champion Bush	14	11*c*	11	8*b*
New Stringless Green Pod	10	9*c*	10	10*c*
Pencil Pod Wax	14	13*c*	10	4*c*
Red Kidney (Dark Mahogany strain)	11	7*c*	8	5*c*
Stringless Kidney Wax	10	9*c*	11	2*b*
Sure Crop Wax	10	9*c*	14	8*b*
Unrivalled Wax	13	2*c*	9	5*c*
Group 3, resistant:				
Corbett Refugee	15	0	16	5*b*
Great Northern Idaho No. 1	10	0	15	0
Robust	10	0	13	0

[1] *b* represents serious infection; *c*, mild infection.

while Corbett Refugee, which is resistant to the former, was susceptible to the latter. Red Valentine, Blue Lake, California White, and Konserva, all susceptible to the common bean mosaic, were resistant to bean mosaic 3. This virus produced severe symptoms on 14 of the 30 varieties tested and mild infection on 10, while 6 were resistant. The common bean mosaic produced severe symptoms on 8 varieties and mild infection on 20, while 3 varieties were resistant.

COMPARISON OF LOCAL LESIONS PRODUCED BY WHITE CLOVER AND ALFALFA VIRUSES WITH THOSE PRODUCED BY OTHER VIRUSES ON BEANS

The production of local necrotic lesions on beans by a virus has been described previously by Wingard (*21*), who reported the tobacco ring spot virus producing local lesions, although no description of the symptoms was given. Price (*14*) records the development of local lesions due to tobacco mosaic on 16 varieties of beans. Zaumeyer and Wade (*24*) reported the production of local lesions on beans inoculated with the mosaic virus of white clover and alfalfa. Pierce (*12*) compared the resistance and susceptibility of beans to the viruses of tobacco mosaic, tobacco ring spot, and alfalfa mosaic.

In order to obtain a comparison between the local lesions produced by tobacco mosaic and tobacco ring spot with those produced by the viruses from alfalfa and white clover, the work of Price (*14*) and Pierce (*12*) was repeated in part. Twenty bean varieties were inoculated with the viruses of tobacco mosaic and tobacco ring spot. The tobacco mosaic produced symptoms identical with those described by Price (*14*). The symptoms due to the tobacco ring spot virus agreed with those described by Pierce (*12*). They appear on the inoculated leaves as necrotic lesions which gradually coalesce with similar spots and finally cause death of the inoculated leaf of certain varieties. The infection later becomes systemic with the final death of the plant. All varieties tested reacted similarly.

The local lesions produced by the alfalfa mosaic virus were brownish red in color, while those produced by the tobacco mosaic virus were dark brown. The lesions caused by the tobacco mosaic virus, according to Price (*14*) and confirmed by the writers, are never more than one-half to 1 mm in diameter, whereas those of alfalfa reached a diameter of 2 mm.

The local lesions produced by the white clover mosaic virus on beans are not identical with those produced by the other two viruses. As mentioned previously, they are larger (2½ to 5 mm in diameter) than those produced by the tobacco and alfalfa mosaic viruses. They may or may not be circular, and the borders are irregular in outline.

Table 3 records the data on the varietal susceptibility and resistance of beans to the viruses of the four hosts mentioned above, which produce local lesions on beans. A complete list of bean varieties is not given, but only those that were inoculated with the four viruses. A more complete list of the varietal reactions to the local lesions of the viruses of white clover mosaic and alfalfa mosaic is given in table 1. The resistance and susceptibility of the varieties to the viruses of tobacco mosaic and tobacco ring spot agree with the data presented by Price (*14*) and Pierce (*12*).

TABLE 3.—*Comparative varietal behavior of bean varieties with regard to local lesions produced by the viruses of white clover mosaic, alfalfa mosaic, tobacco mosaic, and tobacco ring spot*

Variety	Reaction to virus of—			
	White clover mosaic	Alfalfa mosaic	Tobacco mosaic	Tobacco ring spot
Black Valentine	Resistant	Susceptible	Resistant	Susceptible.
Bountiful	Susceptible	do	do	Do.
Burpee Stringless Green Pod	do	do	do	Do.
Corbett Refugee	Resistant	Resistant	Susceptible	Do.
French Horticultural	Susceptible	Susceptible	Resistant	Do.
Full Measure	do	do	Susceptible	Do.
Giant Stringless Green Pod	do	do	Resistant	Do.
Great Northern Idaho No. 1	Resistant	do	Susceptible	Do.
Konserva	Susceptible	Resistant	Resistant	Do.
Low Champion Bush	do	Susceptible	do	Do.
New Stringless Green Pod	do	do	do	Do.
Pencil Pod Black Wax	do	do	do	Do.
Robust	Resistant	do	Susceptible	Do.
Red Kidney (Dark Mahogany strain)	Susceptible	do	Resistant	Do.
Refugee Wax	Resistant	do	Susceptible	Do.
Stringless Green Refugee	Susceptible	do	do	Do.
Stringless Kidney Wax	do	do	Resistant	Do.
Sure Crop Wax	do	do	do	Do.
Tennessee Green Pod	do	do	do	Do.
Unrivalled Wax	do	do	Susceptible	Do.

Decided variations are noted in the susceptibility of the different varieties of beans to the various mosaic diseases producing local lesions (table 3). Of the 20 varieties inoculated, 7 are susceptible to the tobacco mosaic virus, all to the ring spot virus, 18 to the alfalfa virus, and 15 to the white clover virus.

Three varieties—Full Measure, Stringless Green Refugee, and Unrivalled Wax—were susceptible to the four viruses. Corbett Refugee, which was resistant to the alfalfa mosaic virus, was susceptible to the viruses of tobacco mosaic and tobacco ring spot. Konserva, also resistant to the alfalfa virus, was resistant to the tobacco virus but susceptible to the tobacco ring spot virus. No variety studied was resistant to all four of the viruses.

TRANSMISSION TO OTHER LEGUMINOSAE

In addition to inoculating a large number of bean varieties, several other species of the genus *Phaseolus*, as well as species in other genera, were inoculated with the viruses of the common bean mosaic, pea mosaic 2, white clover mosaic, white sweetclover mosaic, alfalfa mosaic, and red clover mosaic. The following Leguminosae were inoculated with these viruses from the regular hosts: Pigeonpea (*Cajanus indicus* Spreng.), knife bean or swordbean (*Canavali gladiata* (Jacq.) DC.), chickpea (*Cicer arietinum* L.), hyacinth-bean (*Dolichos lablab* L.), sweet pea (*Lathyrus odoratus* L.), lentil (*Lens esculenta* Moench), white lupine (*Lupinus albus* L.), alfalfa (*Medicago sativa* L.), white sweetclover (*Melilotus alba* Desr.), tepary bean (*Phaseolus acutifolius latifolius* Freeman), adzuki bean (*P. angularis* (Willd.) W. F. Wight), mung bean (*P. aureus* Roxb.), rice bean (*P. calcaratus* Roxb.), lima bean (*P. lunatus macrocarpus* Benth.), civet bean (Henderson bush variety) (*P. lunatus* L.), urd bean (*P. mungo* L.), pea (*Pisum sativum* L.), soybean (*Soja max* (L.) Piper), velvetbean (*Stizolobium deeringianum* Bort), white clover (*Trifolium repens* L.)

red clover (*T. pratense* L.), broadbean (*Vicia faba* L.), vetch (*V. americana* Muhl.), asparagus-bean (*Vigna sesquipedalis* (L.) Fruwirth), and cowpea (*V. sinensis* (L.) Endl.). The plants were inoculated in the usual manner by rubbing the leaves with the different virus extracts. Table 4 gives the results of these inoculations.

TABLE 4.—*Susceptibility of various legumes to the mosaic viruses of the common bean, pea 2, white clover, white sweetclover, alfalfa, and red clover*

Host	Reaction to virus of—[1]											
	Pea mosaic 2		White clover mosaic		White sweetclover mosaic		Alfalfa mosaic		Red clover mosaic		Common bean mosaic	
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected
	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number
Cajanus indicus (pigeon-pea)	9	0	9	0	8	2	8	0	10	0	9	0
Canavali gladiata (knife bean)	5	0	6	0	4	0	5	0	6	0	6	0
Cicer arietinum (chick-pea)	11	5	19	7	19	15	10	0	22	5	10	0
Dolichos lablab (hyacinth-bean)	10	0	20	0	10	0	9	0	10	0	10	0
Lathyrus odoratus (sweet pea, Baltimore Rose variety)	10	6	20	20	18	17	10	10	20	19	14	0
Lens esculenta (lentil)	15	10	23	22	24	19	------	------	18	18	23	0
Lupinus albus (white lupine)	10	0	9	0	10	0	9	0	8	0	8	0
Medicago sativa (alfalfa)	5	0	5	2	5	0	5	3	5	0	5	0
Melilotus alba (white sweetclover)	9	5	8	7	9	9	10	8	12	0	10	0
Phaseolus acutifolius latifolius (tepary bean)	10	0	8	0	8	0	10	0	8	0	8	0
P. angularis (adzuki bean)	8	7	9	0	10	0	10	8	11	0	10	0
P. calcaratus (rice bean)	18	0	19	0	17	0	16	6	18	0	9	0
P. aureus (mung bean)	10	6*d*	15	12*d*	12	4*d*	10	6*d*	14	14*d*	10	0
P. lunatus macrocarpus (lima bean)	9	0	10	0	9	0	10	0	8	0	10	0
P. lunatus (civet bean, Henderson bush variety)	8	0	10	8	9	0	8	0	8	0	6	0
P. mungo (urd bean)	10	0	8	5*d*	10	0	9	2*d*	10	0	8	0
Pisum sativum (pea, Dwarf Telephone variety)	15	8	20	20	20	20	10	0	15	9	20	0
Soja max (soybean)	10	0	11	0	12	0	8	0	12	0	14	0
Stizolobium deeringianum (velvetbean)	7	0	8	0	6	0	6	0	8	0	7	0
Trifolium repens (white clover)	5	3	5	3	5	0	5	0	5	0	5	0
T. pratense (red clover)	5	0	5	5	5	5	5	3	5	2	5	0
Vicia faba (broadbean)	10	8	10	10	10	10	9	6	10	8	10	0
V. americana (vetch)	12	0	10	10	10	9	10	6	12	11	8	0
Vigna sesquipedalis (asparagus-bean)	10	0	11	0	12	0	9	0	10	0	10	0
V. sinensis (cowpea)	10	0	9	0	10	0	10	0	9	0	10	0

[1] *d* represents local lesions.

Previous investigators have tested many of these species with the common bean mosaic. Reddick and Stewart (*15*) report *Phaseolus lunatus macrocarpus*, *P. acutifolius latifolius*, and *Vicia faba* as being susceptible to the common bean mosaic. Fajardo (*7*) was unable to transmit the virus of bean mosaic to other leguminous hosts. Nelson (*11*) found that in addition to the three species reported by Reddick

and Stewart the following were also susceptible to the common bean mosaic: *Phaseolus calcaratus, P. lunatus, P. angularis, P. coccineus,* and *Vigna sesquipedalis.* He did not inoculate these hosts artificially, but relied on natural insect dissemination in the field.

Pierce (*12*) confirmed the results of Reddick and Stewart (*15*) and also some of those reported by Nelson and in addition was able to infect *Phaseolus aureus, Lespedeza striata* (Thunb.) Hook. and Arn., and *Vicia sativa* L.

The writers have been unable to confirm the results of these investigators, which may have been due to differences in varieties within a species. *L. striata* and *V. sativa* were not used in these tests. In a number of instances mild mottling was observed but the symptoms were not definite enough to establish their susceptibility.

As can be seen from table 4, the host range of the several virus diseases shows considerable variation. Pea mosaic virus 2 infects *Phaseolus angularis, P. aureus, Cicer arietinum, Lathyrus odoratus, Lens esculenta, Melilotus alba, Pisum sativum, Trifolium repens,* and *Vicia faba.*

White clover mosaic was infectious to *Phaseolus aureus, P. lunatus, P. mungo, Cicer arietinum, Lathyrus odoratus, Lens esculenta, Medicago sativa, Melilotus alba, Pisum sativum, Trifolium repens, T. pratense, Vicia faba,* and *V. americana.*

The hosts susceptible to white sweetclover mosaic are the same as those of white clover mosaic except that the virus of white sweetclover also infected *Cajanus indicus* but not *Trifolium repens, Medicago sativa,* or *Phaseolus lunatus.*

Alfalfa mosaic virus showed variations in host susceptibility in comparison with the viruses of white clover and white sweetclover. Infection was secured on *Phaseolus angularis, P. calcaratus, P. aureus, P. mungo, Lathyrus odoratus, Medicago sativa, Melilotus alba, Trifolium pratense, Vicia faba,* and *V. americana.*

The red clover mosaic virus reacted similarly to the viruses of white clover and white sweetclover. It was infectious to all of the hosts that were susceptible to the viruses of these two clovers, with the exception of *Phaseolus lunatus, P. mungo, Cajanus indicus, Medicago sativa, Melilotus alba,* and *Trifolium repens.*

The various hosts reacted differently to the several viruses. The viruses of pea mosaic 2, white clover, white sweetclover, and red clover were, in general, infectious to the same hosts. The alfalfa mosaic virus varied from these four viruses in host behavior.

The viruses of pea mosaic 2, white clover, white sweetclover, and red clover caused death to both *Cicer arietinum* and *Lens esculenta* without the production of any distinctive mottle symptom. On *Phaseolus aureus* and *P. mungo* the mosaic viruses of pea 2 and of these three clovers produced local lesions on the inoculated leaves. The symptoms first appeared as small irregular brown spots from 0.5 to 2 mm in diameter. Later the lesions coalesced, forming large irregular blotches slightly darker in color than in the earlier stages, and covering in some cases as much as one-fourth of the leaf area.

In general, the symptoms produced on a single host by the various viruses are alike. However, the several viruses when inoculated to the various hosts may produce decidedly different symptoms; as, for example, pea mosaic 2 produces local lesions on *Phaseolus aureus*

and systemic lesions on the other hosts that it infects. It appears that none of the species used in these inoculations can be used successfully as differential hosts in readily distinguishing the several viruses, a method that has been shown to be very effective and helpful in the separation of the mosaic virus complexes of other host plants.

Most of the outstanding differences in host reaction of the several viruses are noted in table 5.

TABLE 5.—*Summarized data showing differences in host behavior with mosaic viruses of the common bean, pea 2, white clover, white sweetclover, alfalfa, red clover, and bean 3, on several hosts*

Mosaic virus	Nature of symptoms on beans [1]		Number of bean varieties		Reaction on—							Seed transmission through beans artificially inoculated
					Phaseolus vulgaris				*Pisum sativum*, Dwarf Telephone	*Lathyrus odoratus*, Baltimore Rose	*Melilotus alba* (white sweetclover)	
	Local	Systemic	Inoculated	Susceptible	Stringless Green Refugee	Corbett Refugee	Robust	Great Northern Idaho No. 1				
Common bean	−	+	31	28	+	−	−	−	+	−	−	+
Pea 2	−	+	31	30	+	+	+	−	+	+	+	−
White clover	+	+	31	29	+	+	+	−	+	+	+	−
White sweetclover	−	+	31	27	+	+	+	−	+	+	+	−
Alfalfa	+	−	31	29	+	−	+	+	−	−	−	−
Red clover	−	−	31	0	−	−	−	−	+	+	+	−
Bean 3	−	+	30	24	+	+	−	−	−	−	−	−

[1] Minus sign (−) indicates no infection; plus (+) indicates infection.

SEED TRANSMISSION

It has not been definitely proved that the viruses of any of the legumes except common bean mosaic are seed-borne, although preliminary evidence indicates that the virus may be carried in the seed of pea and white sweetclover in small percentages. Since the common bean mosaic is seed-borne, it was of interest to learn whether the viruses of other legumes, when inoculated to bean, would be so transmitted. Unfortunately, seed from beans infected with pea mosaic 2 and alfalfa mosaic was not collected, but that from plants infected with the mosaic disease of white clover and white sweetclover was. The seed of these plants was planted both in the greenhouse and in the field and allowed to grow to maturity, but in no case did any of the plants become diseased. Likewise, seed collected from *Vicia faba* plants infected with the viruses of these two clover mosaics as well as that of red clover mosaic produced healthy plants.

Larger populations of plants from seed from infected plants are necessary for testing before it can be definitely said that these mosaic diseases are not carried through the bean seed, but the evidence indicates that they are not.

PROPERTIES OF THE VIRUSES

Although the properties of the common bean mosaic were studied by Fajardo (7) and those of an alfalfa mosaic by Pierce (*12*), these studies were repeated in part in order to compare them with the properties of the viruses of pea mosaic 2, white clover, and white

sweetclover. The properties of the common bean mosaic, pea mosaic 2, and white sweetclover mosaic were based on the systemic lesions they produced on Stringless Green Refugee beans. The determinations of the white clover virus were based on the production of both systemic and local lesions on this same variety. The properties of the alfalfa virus were determined by local lesion production on the Red Valentine variety of beans.

The methods described by Johnson and Grant (*9*) were, in general, used for these determinations. In most cases 15 plants were inoculated except in some instances where 25 plants were used. The material for the thermal death-point studies was prepared by heating 2 cc of the expressed juice in thin glass tubes in a constant temperature bath at the desired temperature for 10 minutes and immediately cooling. The aging tests were conducted by placing the expressed juice in test tubes and allowing them to remain in the laboratory at room temperatures (75° to 80° F.) for the desired period. The dilution studies were made in the usual manner. The chemical tests were made by diluting the juice from diseased plants to the proper concentration of the chemical desired and allowing it to react for 30 minutes.

THERMAL DEATH POINT

The virus of the common bean mosaic was inactivated at about 58° C. (table 6), which confirms the results of Fajardo (*7*) and Pierce (*12*). The viruses of pea mosaic 2 and white sweetclover were also noninfectious at this temperature. The virus of white clover mosaic producing the systemic lesions on beans was inactivated at 58° to 60°, and the virus producing the local lesions at 62° to 65°. The alfalfa virus was inactivated at the same temperature, which agrees with the results of Pierce (*12*).

TOLERANCE TO DILUTION

The viruses of the common bean mosaic, pea mosaic 2, and white sweetclover mosaic were not infectious at dilutions greater than 1 to 1,000 (table 7). The virus of white clover mosaic producing the systemic and local lesions on beans and the alfalfa virus lost their infectivity at about 2 to 1,000 dilution.

LONGEVITY IN VITRO

The viruses of the common bean mosaic and white sweetclover mosaic were not infectious after aging in vitro from 28 to 32 hours (table 8). This is in agreement with Pierce (*12*) with respect to the common bean mosaic. The virus of pea mosaic 2 was inactivated at 24 to 28 hours. The white clover virus producing the systemic lesions on beans lost its infectivity after aging about 32 hours, whereas the virus producing the local lesions was inactivated at from 28 to 32 hours. The alfalfa virus was noninfectious at from 3 to 4 days' aging.

TABLE 6.—*Comparison of thermal death point of viruses of common bean mosaic, pea mosaic 2, white clover mosaic, white sweetclover mosaic, and alfalfa mosaic, as determined by production of systemic and local lesions on beans*

Temperature (° C.)	Reaction to virus of—													
	Common bean mosaic		Pea mosaic 2		White clover mosaic					White sweetclover mosaic		Alfalfa mosaic		
					Systemic infection		Local infection		Total lesions			Local infection		Total lesions
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected		Plants inoculated	Plants infected	Plants inoculated	Plants infected	
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Not heated	15	12	15	12	15	12	15	15	[1] 3,715	15	15	15	15	[2] 1,347
54	15	10	15	13	15	10	-----	-----	-------	15	15	15	15	981
56	15	7	15	7	15	8	-----	-----	-------	15	6	15	15	601
58	15	0	15	0	15	9	15	15	3,692	15	0	15	15	298
60	-----	-----	-----	-----	15	0	15	15	3,180	-----	-----	15	13	105
62	-----	-----	-----	-----	-----	-----	15	15	2,718	-----	-----	15	10	26
65	-----	-----	-----	-----	-----	-----	15	0	0	-----	-----	15	0	0

[1] Total number of lesions produced on 30 inoculated primary leaves of Refugee Green bean variety.
[2] Total number of lesions produced on 30 inoculated primary leaves of Red Valentine bean variety.

TABLE 7.—*Comparison of tolerance to dilution of viruses of common bean mosaic, pea mosaic 2, white clover mosaic, white sweetclover mosaic, and alfalfa mosaic, as determined by production of systemic and local lesions on beans*

Dilution	Reaction to virus of—													
	Common bean mosaic		Pea mosaic 2		White clover mosaic					White sweetclover mosaic		Alfalfa mosaic		
					Systemic infection		Local infection		Total lesions			Local infection		Total lesions
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected		Plants inoculated	Plants infected	Plants inoculated	Plants infected	
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
None	15	11	15	11	15	15	15	15	[1] 2,480	15	15	15	15	[2] 795
1 to 10	15	11	15	14	15	15	-----	-----	-------	15	15	15	15	690
1 to 100	15	8	15	8	15	15	-----	-----	-------	15	14	15	15	221
1 to 200	15	4	15	5	15	14	-----	-----	-------	15	5	15	13	87
1 to 400	25	2	25	3	25	13	15	13	35	25	4	15	9	28
1 to 800	25	1	25	3	25	12	15	13	18	25	2	15	3	18
1 to 1,000	25	0	25	0	25	6	15	13	13	25	0	15	4	12
1 to 2,000	-----	-----	-----	-----	25	1	15	2	3	-----	-----	15	2	5

[1] See footnote 1 to table 6.
[2] See footnote 2 to table 6.

TABLE 8.—*Comparison of resistance to aging of viruses of common bean mosaic, pea mosaic 2, white clover mosaic, white sweetclover mosaic, and alfalfa mosaic, as determined by production of systemic and local lesions on beans*

Time aged	Reaction to virus of—													
	Common bean mosaic		Pea mosaic 2		White clover mosaic					White sweetclover mosaic		Alfalfa mosaic		
					Systemic infection		Local infection					Local infection		
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Total lesions	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Total lesions
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
None	15	13	15	11	15	12	15	15	[1] 2,715	15	11	15	15	[2] 1,710
20 hours	15	11	15	4	15	7	-----	-----	-----	15	8	-----	-----	-----
24 hours	15	4	15	3	15	8	15	11	54	15	7	-----	-----	-----
28 hours	15	1	15	0	15	4	15	3	24	15	5	-----	-----	-----
32 hours	15	0	-----	-----	15	2	15	0	0	15	0	-----	-----	-----
2 days	-----	-----	-----	-----	15	0	-----	-----	-----	-----	-----	15	12	17
3 days	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	15	2	2
4 days	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	15	0	0

[1] See footnote 1 to table 6.
[2] See footnote 2 to table 6.

RESISTANCE TO CHEMICALS

The common bean mosaic virus was inactivated by 1 to 200 hydrochloric acid (35 to 37 percent) for 30 minutes (table 9). The viruses of pea mosaic 2, white sweetclover, alfalfa, and the virus of white clover producing the systemic lesions on beans were inactivated by 1 to 100 hydrochloric acid solution, while the virus of white clover producing the local lesions was still infectious at this concentration. The common bean mosaic virus lost its infectivity when treated with 50-percent alcohol. Pea virus 2, white clover mosaic virus, and white sweetclover mosaic virus were inactivated with 75-percent alcohol, whereas the alfalfa virus was still infectious at this concentration. The virus of common bean mosaic, that of white clover mosaic producing the systemic lesions on beans, and that of white sweetclover mosaic were not infectious when treated with a 1 to 500 solution of 37-percent formaldehyde. The virus of pea mosaic 2 was inactivated with a 1 to 1,000 dilution. The white clover virus producing the local lesions on beans and the alfalfa virus were inactivated with a 1 to 200 formaldehyde solution.

TABLE 9.—*Comparison of resistance to chemicals of viruses of common bean mosaic, pea mosaic 2, white clover mosaic, white sweetclover mosaic, and alfalfa mosaic, as determined by production of systemic and local lesions on beans*

Chemical [1]	Strength of chemical	Reaction to virus of—													
		Common bean mosaic		Pea mosaic 2		White clover mosaic					White sweetclover mosaic		Alfalfa mosaic		
						Systemic infection		Local infection					Local infection		
		Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Total lesions	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Total lesions
		No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
None		15	12	15	11	15	13	15	15	[2] 2,480	15	14	15	15	[3] 3,262
Hydrochloric acid	1 to 500	15	6	15	4	15	12	15	14	108	15	5	15	15	275
Do	1 to 200	15	0	15	2	15	7	15	7	7	15	6	15	4	4
Do	1 to 100	----	----	15	0	15	0	15	2	2	15	0	15	0	0
Alcohol	25 percent	15	5	15	7	15	11	15	15	-------	15	8	15	15	3,228
Do	50 percent	15	0	15	4	15	7	15	15	742	15	4	15	15	566
Do	75 percent	----	----	15	0	15	0	15	0	0	15	0	15	14	120
Formaldehyde [4]	1 to 2,000	15	10	15	7	15	6	----	----	-------	15	3	----	----	------
Do	1 to 1,000	15	4	15	0	15	6	----	----	-------	15	1	15	15	2,610
Do	1 to 500	15	0	----	----	15	0	15	15	139	15	0	15	15	1,902
Do	1 to 200	----	----	----	----	----	----	15	0	0	----	----	15	0	0

[1] 30-minute treatments.
[2] See footnote 1 to table 6.
[3] See footnote 2 to table 6.
[4] Concentrated solution containing 37-percent formaldehyde.

DISCUSSION

The evidence presented in this paper shows that the viruses of certain legume mosaic diseases can be transmitted to beans, and that under certain conditions, especially in the field, the symptoms of some may be mistaken for the common bean mosaic. Under controlled conditions in the greenhouse little difficulty is experienced in distinguishing the various diseases when the viruses are inoculated to bean. The more susceptible varieties, such as Stringless Green Refugee, are especially suitable for such diagnostic purposes. Furthermore, there is a definite varietal behavior to the several viruses which serves as a further means of differentiating between them.

It has been demonstrated by the senior writer (*23*) that several species of aphids are capable of transmitting the common bean mosaic virus, and it is probable that they are responsible for most of the secondary spread of the disease in the field. That some of this secondary spread may be caused by aphids transmitting certain of the legume mosaic viruses to bean is entirely probable. It seems likely that aphids feeding on mosaic-diseased legumes growing in close proximity to beans may transmit the virus to bean. The extent of this spread is not known, but in some cases it might be considerable. It may tend to explain why under certain conditions a field containing an extremely small amount of primary mosaic infection in the early part of the growing season may at the end be very severely infected.

Field examinations in many sections of the country have shown that the mosaic diseases of some of the clovers are probably present wherever the hosts are found. In many of the bean-growing sections of the United States the sweetclovers are not only grown as cultivated crops but are also found growing in abundance along the highways, irrigation ditches, and fence rows.

Some of the clovers belonging to the genus *Trifolium* are found almost everywhere in the United States where beans are grown. No systematic search has been made for the occurrence of the mosaic diseases of the legumes already discussed; however, some were found without difficulty wherever searches were made.

The symptoms of the mosaic-infected legumes are more easily recognized in the spring and in early summer than later in the season. In the case of peas grown at high altitudes, the mosaic symptoms are best recognized later in the summer. In general the diseases do not appear to stunt the plant, except possibly pea and bean, and then only when the infection occurs early in the development of the plant. Severely infected white and yellow sweetclover plants may be stunted in the spring, but later in the season they appear to be almost as vigorous as normal plants.

Pea mosaic is not so wide-spread as common bean mosaic. Pea mosaic virus 1 has been found by the writers in Maryland, Montana, Washington, and California. Linford [5] in a survey of pea diseases, found mosaic in nine States, extending from the Atlantic coast west to Utah and Montana. He stated that in Maryland and New Jersey it reached its maximum in both abundance and severity. Pea mosaic virus 2 has as yet been found only in Maryland and Colorado, and it is believed to be less wide-spread than the common pea mosaic virus. In the canning sections of the Eastern and Middle Western States peas are usually removed from the land before the beans in the vicinity have grown to appreciable size, and hence the danger of spread from peas infected with virus 2 to beans is remote except where crop sanitation is not practiced. In the seed and market garden growing areas of the western United States peas are seldom grown in the same localities where beans are produced, which eliminates the probability of mosaic infection from that source.

White sweetclover mosaic is found abundantly in the District of Columbia and in the contiguous sections of Maryland and Virginia. It is probably equally as wide-spread in other parts of these two States. It has also been found in Wisconsin, Iowa, Nebraska, and Colorado. Surveys made in other States most likely would reveal the occurrence of the disease in them.

White clover mosaic is possibly as wide-spread as white sweetclover mosaic, but because the symptoms are somewhat inconspicuous it may be easily overlooked. It has been found wherever sought, but since white clover is not commonly grown in the Western States, it is of little importance there, and would not be a factor in the spread of its mosaic to beans. In the eastern and middle western bean-growing sections it may be a more important factor.

Alfalfa mosaic does not appear to be as wide-spread as the virus diseases of white clover and white sweetclover. A careful search has been made in the East and in some of the intermountain States,

[5] LINFORD, M. B. PEA DISEASES IN THE UNITED STATES IN 1928. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Reptr. Sup. 67: 1–14. 1929. [Mimeographed.]

but only a small amount was found. Under high temperatures the symptoms are masked, and since the inspections were made in the summer it is likely that it was present but its symptoms were masked. Under California conditions, Weimer (*20*) reports it as being especially abundant in the spring of the year before the first cutting.

In the spring of 1931 white sweetclover mosaic was found very abundantly in the vicinity of Rosslyn, Va., and marked symptoms were noted on practically all second-year growth. Preliminary evidence indicates that this mosaic is not seed-borne, but if so it is only in small amounts. The virus apparently overwinters in the roots of the plant and appears in the first growth in the spring. Aphids are commonly found feeding on such plants and probably transfer the virus to seedlings.

The rapidity and ease with which white sweetclover mosaic may be transmitted from plant to plant was demonstrated under greenhouse conditions. In the fall of 1932 about 200 healthy seedlings were planted in a greenhouse bench. The house was fumigated regularly until May, at which time most of the experimental work was terminated. At this time about 5 percent of the plants were inoculated and produced typical symptoms. The plants were allowed to grow during the summer, but no precaution was taken to control aphids. In the fall of 1933 all the plants were infected, the disease probably having been spread by the aphids feeding on the plants during the summer. It is assumed that the disease is spread in this manner under field conditions from the biennial plant to the seedlings and hence is present every year.

White clover mosaic does not appear to be spread as readily as white sweetclover mosaic, since initially infected areas do not enlarge very rapidly. Aphids are found on this clover, but seldom in large numbers. The virus appears to overwinter in the roots as it does in white sweetclover, and reappears in the new growth in the spring.

It has already been pointed out that red clover mosaic is not transmissible to beans, although it was shown by Doolittle and Jones (*4*), and substantiated by the writers, that it is transmissible to peas and sweet peas. Doolittle and Jones stated that it seems probable that red clover acts as a source of mosaic infection to peas in the field.

It is quite likely that pea mosaic virus 1, which is not infectious to beans, may have been the same as the one reported by Doolittle and Jones (*4*) and may be identical with red clover mosaic. The fact that pea mosaic virus 2 was infectious to beans clearly shows that there are at least two forms of mosaic found on peas, and further studies may demonstrate more.

The symptoms of red clover mosaic are not all alike. In fact, they may be so variable as to indicate the possibility of more than one form. Preliminary studies on peas have indicated that there may be two forms, but a more detailed study of the viruses is necessary before any definite conclusions can be drawn. Whether all forms of pea mosaic are actually identical with one or the other of the clover mosaic diseases transmitted to peas is still unknown. Doolittle and Jones (*4*) were unsuccessful in transmitting the mosaics of sweetclover and bean to garden peas and sweet peas. The writers, on the other hand, transmitted the mosiac diseases of white sweetclover and white clover to pea and sweet pea. The symptoms pro-

duced on pea by these two viruses were indistinguishable from those caused by the pea viruses 1 and 2. They can be identified, however, by means of a cross inoculation to beans, where symptoms identical to those produced by the viruses of the specific hosts are produced.

Results indicate that there may be more than one form of white clover mosaic, as shown by inoculation studies with beans and peas. White clover mosaic was obtained from several sources. Two specimens collected in the Eastern States gave identical results in that both produced local and systemic infection as previously described. Specimens collected in Colorado produced no local lesions, and the systemic lesions on Stringless Green Refugee beans somewhat resembled the symptoms produced by pea mosaic virus 2 except that the infection was not so severe.

The production of local and systemic lesions on beans by white clover mosaic suggests the possibility of two distinct viruses, one producing local and the other systemic lesions. Numerous sources of white clover mosaic were used in the experimental work, with similar results.

Since many of the clover mosaic viruses can be transmitted to other leguminous hosts, it is likely that infection studies alone might be misleading. The study of symptoms on susceptible bean varieties, and of the reaction to these viruses of the varieties resistant to the common bean mosaic, is helpful in separating them. That more than one virus may infect a single host is possible. Since white sweetclover is susceptible to white clover mosaic, it might harbor both viruses at the same time. Two or more viruses combined on one host might produce symptoms on beans different from those reported here. From this it is apparent that symptomatology is not alone sufficient in the diagnosis of virus diseases of many of the legumes, but that a study of the particular virus as to host reaction and properties becomes essential.

There have been a number of reports showing that in addition to the common bean mosaic other viruses are capable of being transmitted to bean. Carsner (*2*) showed that the virus of curly top of sugar beets is transmissible to beans. Nelson's rugose mosaic of beans (*11*) appears to be different from any of the virus diseases reported here, especially on the basis of seed transmission. Pierce's yellow bean mosaic (*12*), on the basis of symptoms, transmission, and properties of the virus, appears to be a form of white sweetclover mosaic described previously by the writers (*24*) and not truly a bean mosaic. It is evident from a comparison of varietal resistance and susceptibility of beans that, although yellow bean mosaic is somewhat similar to the white sweetclover mosaic described here, it is not identical therewith. Pierce (*12*) reports that no varieties of the common bean have been found which are entirely resistant to the yellow bean mosaic. It is possible that these differential reactions may be due to the various bean strains employed.

Data presented here show that Great Northern Idaho No. 1, Robust, California White, and Red Kidney (Dark Mahogany strain) beans are resistant to the white sweetclover mosaic virus. Pierce reported no test on the last two varieties, but found the Great Northern Idaho No. 1 and Robust varieties susceptible to yellow

bean mosaic. Yellow bean mosaic was reported to be noninfectious to peas (Perfection variety). The writers, however, found the white sweetclover mosaic to be readily transmitted to this variety.

Merkel (*10*) in his transmission work with aphids concluded that the same virus was responsible for the mosaic of *Phaseolus vulgaris, Pisum sativum, Lathyrus odoratus, Lupinus luteus, Melilotus altissima, Trifolium pratense, T. hybridum, T. repens, Anthyllis vulneraria,* and *Vicia faba.* It is apparent from the writers' data that more than a single virus is responsible for the mosaic diseases of these legumes.

Elliott's (*5*) mosaic virus of sweetclover and red clover was shown by him to be mutually transmissible as well as infectious to *Medicago arabica* and *Vicia faba.* He was unable, however, to infect *Trifolium repens* with it. This virus does not appear to be the same as that causing the mosaic disease of white sweetclover and red clover reported here, because of the inability of these two viruses to be cross-inoculated. The virus of red clover has been shown by Dickson (*3*) to be transmissible to a number of species of the genus *Trifolium* and to *Medicago lupulina,* but not to *Melilotus alba* or to *M. officinalis.* This mosaic may be similar to the red clover mosaic reported here but different from the pea mosaic virus 2, which, as has been pointed out, is not identical with the pea mosaic described by Doolittle and Jones (*4*). Böning's virus disease from broadbean (*1*), which he was able to transmit to red clover, crimson clover, and peas, may be identical with the pea mosaic virus 1 and the red clover mosaic reported by the writers. It may also be identical with the pea mosaic of Doolittle and Jones (*4*). Pierce (*12*) states that the alfalfa mosaic described by him was distinct from the mosaic studied by Weimer (*19, 20*) and later by the writers (*22, 24*). The differences were not pointed out. Weimer's alfalfa mosaic differs from the one discussed by Pierce (*12*) in its reaction to Corbett Refugee bean and to peas. Pierce states that Corbett Refugee is slightly susceptible to his alfalfa mosaic, whereas the writers were unable to infect this variety. He also reports peas as being susceptible, while negative results were secured with the alfalfa mosaic used in the studies reported here. Since these differences are slight, it is not unlikely that Pierce's alfalfa mosaic is identical with Weimer's, as reported earlier by the writers (*22, 24*) as infecting beans.

Henderson's ring spot of sweetclover (*8*), which he transmitted to Turkish tobacco and petunia, is distinct from the white sweetclover mosaic reported here. The symptoms of this disease on white sweetclover differ from those of the mosaic disease of this host.

As yet little is known regarding the economic importance of the spread of the legume mosaics to bean. It is believed that they are responsible for considerable losses. Because of the similarity, under certain conditions, of symptoms between the common bean mosaic and certain of the legume mosaics on bean, it is not unlikely that they have been mistaken for bean mosaic. Since the mosaic viruses of white clover and white sweetclover on bean have not been proved thus far to be seed-borne, it appears that they will never reach the importance of the common bean mosaic. The location of the bean plot so as not to be in close proximity to cultivated legumes, especially the clovers, and the eradication of those growing wild, may be helpful

in controlling, at least in part, the secondary spread of these virus diseases to beans.

The development by selection of varieties resistant to the common bean mosaic (Corbett Refugee, Great Northern Idaho No. 1, and Robust) has been accomplished. These varieties have been used as parental stock in the production of other varieties of the canning and market-garden types resistant to the common bean mosaic. It is possible that varieties resistant to all of the legume mosaic diseases can be developed. The facts that Great Northern Idaho No. 1 is resistant to most of these diseases and Corbett Refugee and Robust are resistant to others offer promising parent material for the development and improvement of other resistant varieties.

SUMMARY

The viruses causing the mosaic disease of pea, white clover, alsike clover, white sweetclover, alfalfa, and sweet pea are all transmissible to beans, while the virus of red clover mosaic is not. The mosaic virus obtained from a bean hybrid proved to be distinct from the common bean mosaic and from any of the clover mosaics.

The symptoms of the mosaic viruses from white clover, alsike clover, and white and yellow sweetclover, when inoculated to bean, may under certain conditions resemble the mottled and chlorotic conditions of the common bean mosaic. However, a careful examination under greenhouse conditions reveals specific differences.

It is probable that various other mosaic viruses present in the several legumes may react differently from those reported in this paper notwithstanding similarity of symptoms.

The legume mosaic viruses produced systemic infection on beans, with the exception of alfalfa virus, which produced only local lesions. The white clover mosaic virus may produce both systemic and local lesions.

The susceptibility and resistance of 31 bean varieties to the viruses of the legumes mentioned were determined. Thirty out of 31 varieties of beans tested were susceptible to the pea mosaic virus 2, and the white clover mosaic virus produced typical symptoms on 29 out of 31 varieties inoculated. The white clover mosaic virus on beans produced local lesions on 26 out of 30 varieties tested. White sweetclover mosaic infected 27 out of 31 varieties. Twenty-nine out of 31 varieties of beans were susceptible to the alfalfa mosaic virus. The virus of bean mosaic 3 infected 24 out of 30 varieties tested.

The three bean varieties resistant to the common bean mosaic do not react identically when inoculated with the viruses of the various legumes. Great Northern Idaho No. 1 is resistant to all of the viruses used except to that of the alfalfa mosaic. Robust is susceptible to the viruses of pea mosaic 2, white clover mosaic, and alfalfa mosaic. Corbett Refugee is resistant only to the alfalfa virus. Bean mosaic virus 3 is infectious only to Corbett Refugee.

The local lesions produced by tobacco mosaic and the tobacco ring spot viruses are different from those produced by the mosaic viruses of white clover and alfalfa, both in symptoms and in varietal susceptibility.

The various leguminous hosts showed differences in resistance and susceptibility when inoculated with the several legume mosaic viruses.

No evidence of transmission of white clover mosaic, white sweetclover mosaic, and bean mosaic virus 3 through bean seed was obtained.

The thermal death point, tolerance to dilution, resistance to aging in vitro, and resistance to chemicals were determined for all the viruses. The thermal death point of the viruses of the common bean mosaic, pea mosaic 2, and white sweetclover mosaic was found to be between 56° and 58° C. The virus of white clover mosaic producing the systemic lesions on beans was inactivated between 58° and 60°, while that producing the local lesions on beans and also the alfalfa virus lost their infectivity at 62° to 65°. As for tolerance to dilution, the viruses of the common bean mosaic, pea mosaic 2, and white sweetclover mosaic were not infectious at dilutions greater than 1 to 1,000. The viruses of white clover mosaic producing both the systemic and local lesions on beans and the alfalfa virus were still infectious at 1 to 2,000 dilution. In experiments on aging in vitro, the virus of the common bean mosaic and white sweetclover mosaic were no longer infectious after 28 to 32 hours; the virus of pea mosaic 2 lost its infectivity at from 24 to 28 hours; that of white clover producing the local lesions on beans was inactivated when aged from 28 to 32 hours, whereas the virus producing the systemic lesions was not infectious after 32 to 48 hours. The alfalfa virus was inactivated after aging for 3 to 4 days. With respect to resistance to chemicals there were certain differences between the various dilutions of hydrochloric acid, alcohol, and formaldehyde.

Pea mosaic virus 2 is not believed to be as wide-spread as the common pea mosaic. Alfalfa mosaic appears to be limited in its dissemination. The mosaic diseases of white clover and white sweetclover have been found in many localities, and it is assumed that they are present wherever the hosts are grown. It is possible that beans may become infected from the various legume mosaic viruses in the field as a result of aphid transmission. Until varieties resistant to these diseases have been developed, bean fields should be located as far from infected commercial clover plantings as possible. The elimination of legumes growing wild along roadways, fence rows, and irrigation ditches may prove an effective control measure.

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RANDOM SAMPLING AND THE DISTRIBUTION OF PHENOTYPES ON EARS OF BACKCROSSED MAIZE [1]

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INTRODUCTION

The distribution of a given phenotype on ears of maize (*Zea mays* L.) segregating for an endosperm character should be purely random if determined by chance alone. In classifying kernels on backcrossed ears the writer gained the definite impression that the distribution was not random. In conversation with other investigators he found that some held a similar opinion and that others thought the distributions were quite random. The data presented here were collected to test the randomness of distributions of two contrasting phenotypes.

MATERIAL AND METHODS

Maize plants of the constitution *Y-y Su-su* were pollinated with *y-su* pollen. This permits the expression of the gametophyte as determined at meiosis in the pistillate inflorescence. The cross made in this way also permits a more accurate separation of yellow (*Y*) and white (*y*) seeds and eliminates any possible disturbing effect of pollen-tube growth factors or differential establishment of pollen tubes.

The phenotype of each kernel for each of 81 ears from this cross was recorded by code, as illustrated in figure 1. The frequencies of groups of 1, 2, 3, etc., individuals were then tabulated. It was originally planned to study the distribution of phenotypes both vertically and laterally on the ear. During the accumulation of the data, however, it became apparent that distribution in the lateral direction might be inaccurate because of spatial changes occurring between meiosis and maturity. The data presented represent the distributions in vertical rows only.

EXPERIMENTAL RESULTS

The contrasting phenotypes, *Y-y* and *Su-su*, are expected to occur with equal frequency. With random distribution the expected number of groups of a stated size will be given by the expression $(.5^n)N$, where n is the number of kernels in the group in question and N is the total number of groups.

Two methods have been used in estimating the randomness of the various distributions. The first estimate used was P, calculated from the χ^2 test. The second method [2] attempts to answer the question whether or not the data are consistent with an independent 1:1 chance for each kernel. If there are a individuals in a set of consecutive kernels, the phenotypic change from one kernel to the next is independently decided $a-1$ times. The number of possible changes in any given population is then $S(a-1)$. If this value differs significantly from half that of $S(a)$, then an independent 1:1 chance for

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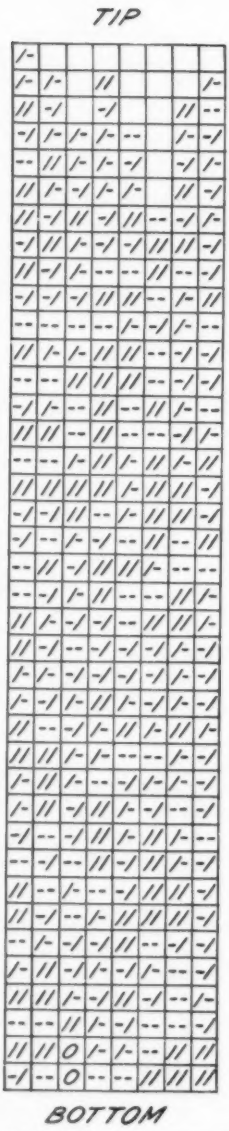
[2] The writer is indebted to R. A. Fisher for suggesting this procedure.



// Y Su.....Yellow Starchy
/- Y su.....Yellow Sugary
-/ y Su.....White Starchy
-- y su.....White Sugary
0.....Missing Kernel

FIGURE 1.—Method of recording the phenotypic constitution of individual kernels on a backcrossed ear of corn.

each kernel has not been realized. The deviations of $\frac{1}{2}S(a)-S(a-1)$ divided by the probable error furnish the second estimating statistic. Hereafter the first method will be designated as the probability method and the second the deviation method.

The observed frequencies for the individual phenotypic classes are presented in table 1. It is quite apparent that the distributions are not random in any case. The distributions of the sum of the yellow-white and starchy-sugary group also are presented. This distribution is merely one of groups of a given size irrespective of phenotype. In both the yellow-white and starchy-sugary combinations the χ^2 values are higher than those of either component distribution. This indicates that the distributions tend to be biased in the same direction. It is apparent that this bias operates to increase the number of groups with one kernel per group and decrease the number of groups with three or more kernels.

TABLE 1.—*Frequencies of phenotypic groups of a given size, and probability of randomness of these frequencies*

Kernels per group (number)	Frequencies of groups of phenotype indicated					
	Y	*y*	*Y+y*	*Su*	*su*	*Su+su*
1	2,522	2,572	5,094	2,532	2,639	5,171
2	1,159	1,155	2,314	1,213	1,148	2,361
3	595	553	1,148	536	522	1,058
4	256	265	521	265	255	520
5	124	111	235	126	117	243
6	67	51	118	50	67	117
7	25	24	49	34	33	67
8	13	17	30	11	11	22
9+	9	14	23	12	11	23
Total	4,770	4,762	9,532	4,779	4,803	9,582
χ^2	30.45	45.89	70.81	36.51	57.96	87.88
P	<0.0002	<0.0002	<0.0002	<0.0002	<0.0002	<0.0002

Missing kernels should occur in the different classes in proportion to the total number of kernels in each class. Twenty-five percent therefore should occur in classes of one individual, 25 percent in classes of two individuals, etc. Missing kernels in the first class will result in an increase in group size because of combining adjacent groups. Groups originally involving two or more kernels but depleted by a single missing kernel will contribute equally to all groups smaller than the one in which the miss occurs. The occurrence of groups of missing kernels, which is noted much more rarely, likewise contributes to the smaller groups, though the contributions may not be equal. The net effect is an increase in the number of one-kernel groups and a decrease of all other size groups.

The distribution of groups adjacent to a missing kernel was tabulated and found to be in general agreement with the expectations outlined above. This indicates that missing kernels is one factor contributing to the bias indicated in table 1, and in consequence correction for missing kernels appears legitimate.

Missing kernels may be corrected for in two ways, by eliminating all kernel rows with missing kernels and by eliminating the groups adjacent to a missing kernel. A priori it would appear that these two methods should be equally effective. The comparative results are presented in table 2.

TABLE 2.—*Estimates of randomness of the frequencies of phenotypic groups after correction is made for missing kernels*

Source of data	Estimating statistic	Values for phenotype indicated					
		Y	*y*	*Y+y*	*Su*	*su*	*Su+su*
Entire data; no correction	*P*[1]	<0.002	<0.002	<0.002	<0.002	<0.002	<0.002
Corrected for missing kernels	*D*[2]	7.92	10.25	12.65	8.9	10.6	13.8
Elimination of groups adjacent to skip[1]	*P*	.29	.25	.04	.07	.06	.01
	D	2.3	4.1	4.5	4.2	5.4	6.5
Elimination of kernel rows containing a skip[2]	*P*	.38	.35	.11	.15	.04	.02
	D	2.0	3.0	3.5	3.4	5.4	6.2

[1] Determined from χ^2. [2] The deviation of $\frac{1}{2}S(a)-S(a-1)$ divided by its probable error.

When the correction for missing kernels is accomplished by eliminating groups adjacent to the skip (table 2, method 1), the distribution for each phenotype is within the limits of random sampling as estimated by *P* determined from χ^2. The fits for the starchy and for the sugary distributions are considerably poorer than those for the yellow and white. In both cases the distribution of the sums gives a poorer fit than either component, indicating that a slight bias still exists.

When the correction for missing kernels is accomplished by eliminating kernel rows with missing kernels (table 2, method 2), the probability for the randomness of all distributions, save one, is slightly higher than when the previous method of correction is used. The differences between the two methods, however, are not significant.

The corrected data indicate that for the starchy-sugary distributions a significant bias still is operative. There is a suggestion that a smaller though similar bias is operative in the yellow-white distributions. The deviations on the basis of an independent 1:1 chance for each kernel are clearly significant.

In the maize ear, judging from the development of the silks, meiosis begins in a region near the base of the ear and proceeds in a regular manner in both directions. The distribution of the end group of each kernel row might conceivably be biased, owing to a possible limitation in size. The possibility was tested by separating the population into two subgroups. One subgroup was composed of the end group of each kernel row, and the other was composed of the remainder of the ear. The results are presented in table 3. The subgroup composed of the end group of the butt and tip of each kernel row is quite random, as indicated by both the probability and the deviation methods. The subgroup composed of the remainder of the ear is clearly not random. The distributions of these two subgroups for the total *Y-y* and *Su-su* phenotypes are compared with theoretical expectancy in figures 2 and 3.

TABLE 3.—*Estimates of randomness of the frequencies of phenotypic groups after separation is made into butt-tip and middle subgroups*

Source of data	Estimating statistic	Values for phenotype indicated					
		Y	*y*	*Y+y*	*Su*	*su*	*Su+su*
Subgroups:							
Butt-tip	*P*[1]	0.49	0.26	0.28	0.76	0.80	0.47
	D[2]	.1	.8	.6	1.7	.3	.4
Remainder	*P*	.51	.09	.02	.04	.002	.001
	D	2.8	5.2	5.4	4.1	6.1	7.0

[1] Determined from χ^2. [2] The deviation of $\frac{1}{2}S(a)-S(a-1)$ divided by its probable error.

A bias which involves all portions of the ear except the end groups might arise through limitations imposed by the length of each kernel row. As an extreme example, a group of 8 kernels could have its point of origin in only three places in a row having only 10 kernels, and only one of these could be included in the subgroup designated as "remainder" in the preceding paragraph. In other words, only 10 percent of the theoretical places of origin can lead to an inner group of eight kernels. A similar but decreasingly important limitation will be noted as longer and longer rows are involved. An estimate of the importance of this limitation was obtained by selecting two subgroups from the total population. One group was composed of ears

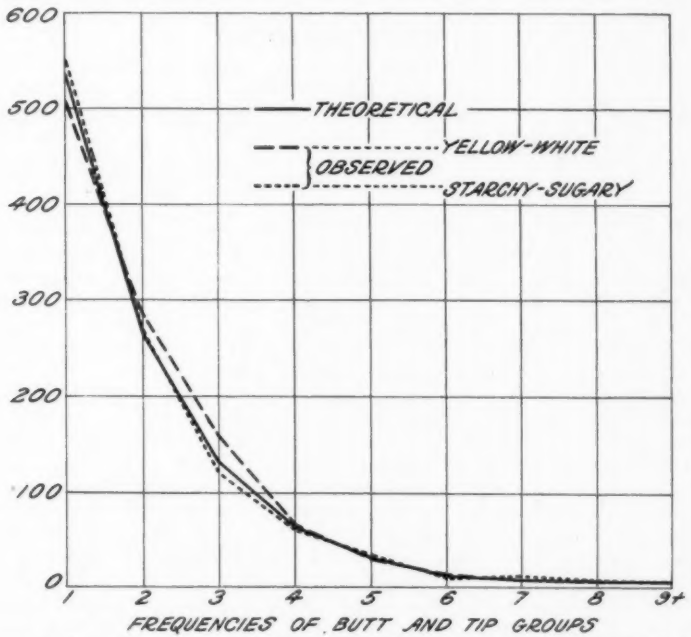


FIGURE 2.—Comparison of observed and theoretical distributions in the subgroup composed of the butt and tip end groups.

having 25 or fewer kernels per row with a mean of 19. The contrasting group had 35 or more kernels per row with a mean of 38. The comparisons are presented in table 4.

TABLE 4.—*Estimates of randomness of the frequencies of phenotypic groups after separation is made into long and short kernel row subgroups*

Source of data	Estimating statistic	Values for phenotype indicated					
		Y	*y*	*Y*+*y*	*Su*	*su*	*Su*+*su*
Subgroups:							
35 or more kernels per row	P [1]	0.06	0.13	0.12	0.50	0.04	0.76
	D [2]	2.80	2.13	2.92	.37	2.57	2.05
25 or fewer kernels per row	P	.06	.14	.08	7.01	.30	.01
	D	3.77	2.78	4.64	6.44	1.72	5.89

[1] Determined from χ^2. [2] The deviation of $\frac{1}{2}S(a)-S(a-1)$ divided by its probable error.

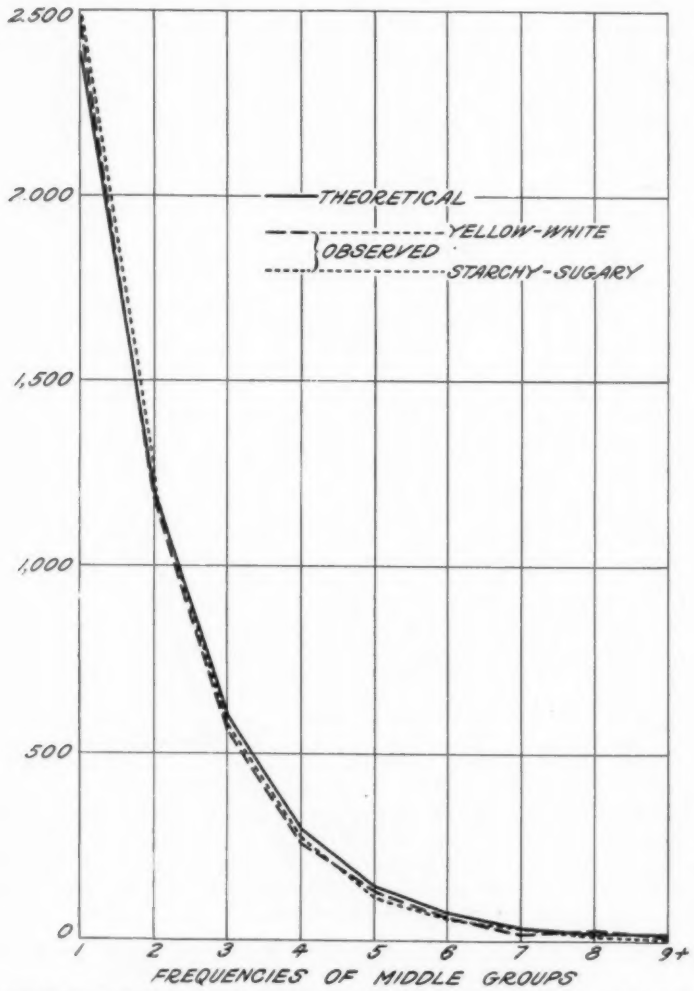


FIGURE 3.—Comparison of observed and theoretical distributions in the subgroup composed of all the ear except the butt and tip end groups.

In the majority of cases the distributions for the ears with longer kernel rows are more nearly in accord with expectancy than for the shorter, though the differences are not great. By a process of combining adjacent end groups when similar in phenotype, it is possible to consider the material from the 81 ears as belonging to a single kernel row and thus eliminate variations due to length of row from ear to ear. This has been done, and the comparison is presented in table 5.

TABLE 5.—*Estimates of randomness of the frequencies of phenotypic groups when the entire population is treated as a single kernel row*

Source of data	Estimating statistic	Values for phenotype indicated					
		Y	*y*	*Y+y*	*Su*	*su*	*Su+su*
All ears combined in 1 kernel row.	P [1]	0.11	0.77	0.10	0.36	0.72	0.95
	D [2]	1.22	.12	.95	.28	1.31	1.29

[1] Determined from χ^2.
[2] The deviation of $\frac{1}{2} S(a)-S(a-1)$ divided by its probable error.

This distribution was also corrected for missing kernels by disregarding groups adjacent to a missing kernel. When this comparison is made the distribution is entirely random as judged by either estimating statistic. This distribution for the *Y–y* segregation is given in figure 4.

The segregation for the contrasting allelomorphs *Y–y* and *Su–su* are in fair agreement with the expected 1:1 distribution as judged by their deviation-probable error values, but there is a slight excess over expectancy of ears having large deviations. A comparison of the relative agreement with expectancy for ears of this group with ears whose deviations are half their probable error or less showed no significant difference between these two subgroups.

The correlation between size of adjacent groups was determined from a double-entry table. In the preparation of this table, butt and tip groups and groups adjacent to a missing kernel were not used. Thus the first and last usable groups of each kernel row were involved in only one comparison, while the intervening groups were used twice. The values of r so calculated were found to be -0.001 ± 0.008 for the *Y–y* and -0.004 ± 0.0123 for the *Su–su* phenotypes. Neither of these values differs significantly from zero, which is the value expected with a purely random distribution.

SUMMARY

The distribution of groups of 1, 2, 3, etc., kernels of the yellow-white and starchy-sugary phenotypes was studied on 81 back crossed ears of maize. The data as originally collected were found not to be random, contrary to expectation.

A bias operated to increase the number of groups with 1 kernel per group and to reduce the number having 3 or more.

Missing kernels and length of kernel row were found to be the chief sources of this bias. When corrections were made for these disturbances, the distributions were well in accord with expectancy.

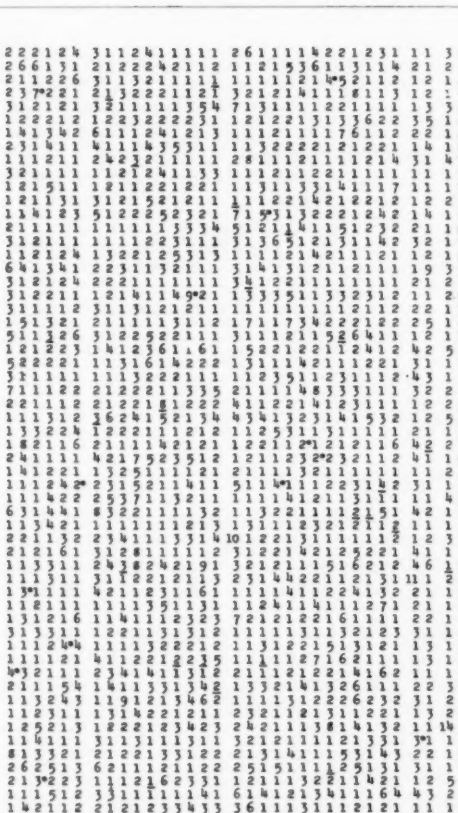


FIGURE 4.—Distribution of the *Y-y* phenotypes from 81 ears considered as being from a single kernel row. Starting at the top of the left column, the distribution proceeds down each column progressively toward the right. The classes marked with an asterisk represent combined classes at the junction between two ears. A horizontal dash between classes indicates a junction between ears in which the end groups were unlike and therefore not combined.

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